"THE DEVELOPMENT OF SOCIAL BEHAVIOR IN IMMATURE MALES OF A FERAL HORSE POPULATION (*Equus caballus*)"

Dissertation

zur Erlangung des Grades eines Doktors
der Naturwissenschaften

der Fakultät für Biologie
der Eberhard - Karls - Universität Tübingen

vorgelegt

von

Rolf Hoffmann

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Dekan	Prof. Dr. E. Kulzer
1.Berichterstatter	Prof. Dr. K. Schmidt-Koenig
2.Berichterstatter	Prof. Dr. P. Klopfer

THE DEVELOPMENT OF SOCIAL BEHAVIOR IN IMMATURE MALES OF A FERAL HORSE POPULATION (*Equus caballus*)

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Dissertation

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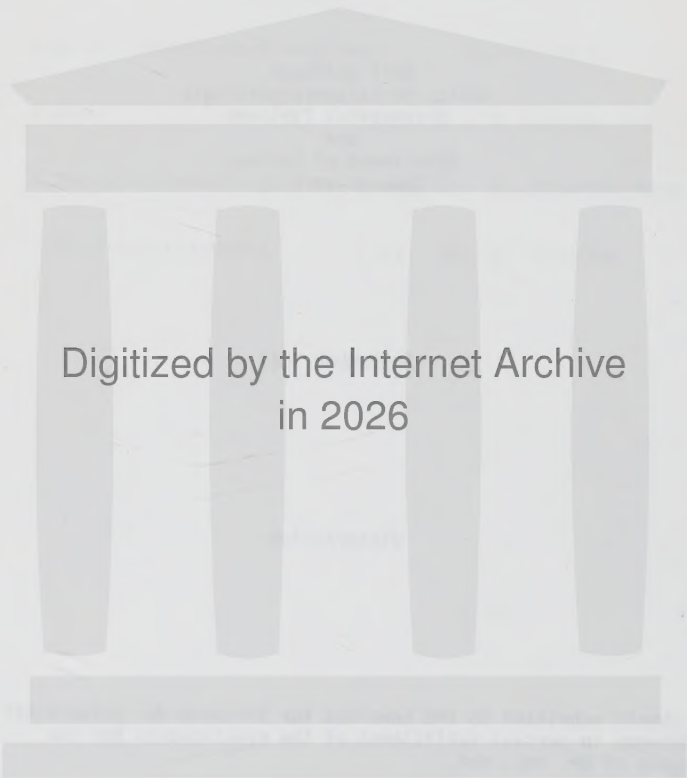
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ABSTRACT

Social behavior was observed almost daily for two consecutive years in all maturing individuals of a feral horse population on an island off the coast of North Carolina, USA. The ontogeny of social behavior was examined with respect to age, sex, and social environment, and was compared with the social behavior of adult horses. Both the frequency and the structure of behavior patterns differed between the sexes after the first year of life. These differences increased with age until both sexes had attained adulthood. In male horses, the development of social behavior was dependent on both social context and age.

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INTRODUCTION

Recent studies of feral and wild Equid populations have paid particular attention to social behavior and organization. Klingel (1969, 1972, 1974) and Joubert (1972) report that populations of plains zebra (Equus quagga boehmi) and mountain zebra (Equus zebra hartmannae) generally consist of harem groups, defended by one stallion, with associated bachelor groups. The social system of Grevy's zebra, on the other hand, seems to be similar to the system of wild asses (Klingel 1974). Neither have harem-like groups; adult animals live singly or in solitary mother-offspring groups. Territories are kept throughout the year by single males, but are defended only in the presence of estrous females. In general, the social system of Grevy's zebra and feral asses also exists in the African (Equus africanus) and Asiatic (Equus hemionus) wild ass. The smallest social units are single mare-foal groups, mares and single males, or bachelors and single yearlings. However, temporary assemblages of all kinds occur frequently (Klingel 1977). 'Super groups' consisting of many adult and immature animals of both sex have been observed during the day. However, during the breeding season, the males will establish large territories which are defended only against other males in the presence of estrous females. Moehlman (1974) reports a similar unstable social organization in feral asses (Equus asinus) in the Death Valley (USA), as does Woodward (1978) for feral asses in the southern deserts of California (USA), and Hoffmann (1983) for feral asses in Central Australia.

Horses (Equus caballus) appear to be the most flexible Equid species. Generally, feral, unmanaged populations of horses show a social system and spatial strategy similar to the system found in the plains zebra and mountain zebra (Imanishi 1953, McKnight 1958, Bruemmer 1967, Rhymer 1970, Feist 1971, Tyler 1972, Welsh 1973, Berger 1977, Miller and Denniston 1979, Hoffmann 1980, and Lenarz 1980, personal communication). Recent studies on feral populations of horses, revealed territoriality (Pollock 1979, personal communication), mixed-sex peer groups (Keiper 1976a, Goldschmidt-Rothschild and Tschanz 1978), and even a totally 'loose' social system, comparable to the system observed in feral asses (Hoffmann 1983).

Aside from their type of social organization, all known Equid species have a surprisingly uniform set of basic social behavior patterns which they use in similar social contexts (Klingel 1972). The observable social behavior of Equid males, under natural conditions, appears much more complex than the social behavior of females. The more complex behaviors are generally observed in intermale and intergroup competition. In all Equid species, males are physically able to, and frequently do, dominate females and offspring (Berger 1983), independent of their social organization. Especially in horses

organized in harem groups, the reproductive success of a population is totally dependent on the male's social, environmental, and spatial strategy. A group stallion determines the size of the group, its daily activity pattern, its spatial arrangements, its resource exploitation, and normally sires all offspring in his harem. A mare's social activity is usually restricted to mother-foal interactions with few social contacts with other group mares (Feist and McCullough 1976, Hoffmann 1980, and Waring 1983).

The development of the two different sex-related roles in Equids is not yet completely understood. In horses, both male and female foals spend the first year of their life in close contact with their mother and her group. Foals leave their maternal groups between the first and second breeding season. Most of the female foals are sexually receptive when they are between 1 and 1½ years old (Klingel 1972, Waring 1983), at which time they join other harem groups (Feist 1971, Tyler 1972, and Hoffmann 1980). In feral populations, young males form unstable assemblages called bachelor groups until they are five to six years old (Alverdez 1925, Klingel 1964, 1965, Feist 1971, Berger 1977, Hoffmann 1980). At this age, they begin to form their own harem groups. Thus, they enter the reproductive stage of life considerably later than do females. On the other hand, male and female foals of a feral horse island population (Hoffmann 1980) did not differ significantly in their observable social behavior and activity. Reports of other feral horse populations indicate the same result (Feist and McCullough 1976, Berger 1977). Therefore, it should be assumed that in feral populations, the development of the complex social behavior of males takes place during bachelorhood, that is, the period they spend in bachelor groups.

In order to gain some understanding of the relation between the Equid social system and the development of the role-specific behavior which controls this system, I will address the following questions.

(1) How does the occurrence, frequency, and distribution of social behavior differ between sexes at different ages?

(2) How does social behavior develop in feral horses?

The presentation of results is divided into five main parts: (1) the observed frequency of occurrence of categories of social behavior (i.e., marking, play, agonistic behavior, etc.) as a function of age in males and females, (2) the frequency distributions (relative frequency of occurrence of the various categories among animals of the same age) over age, in males with different social context, and in females, (3) the completion of social behavior (see page 33), (4) the variability in the age-specific social behavior, and (5) the age at first occurrence of all individual behavior patterns in males and females of this population.

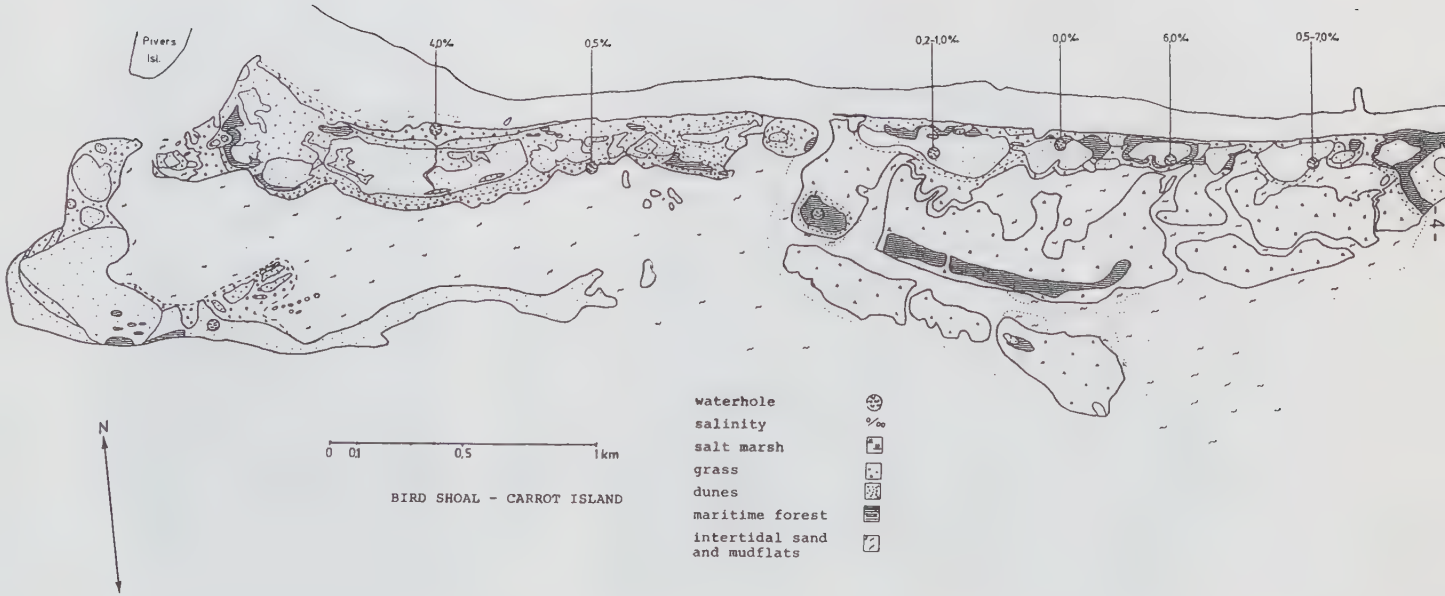
STUDY AREA

This project was conducted with a population of feral horses on Bird Shoal-Carrot Island off the coast of North Carolina, USA. The island is a narrow complex of salt marsh, intertidal sand, mud flats, dredge spoils, and patches of maritime forest separated by intertidal creeks. It is approximately six kilometers long and between 0.5 and 1 kilometer wide, and stretches from east to west. The northern part of the island consists mainly of sand dunes separated by laurel, blue jack oak, and juniper forests. The middle part of the eastern half of the island is composed of intertidal salt marsh, bordered to the south by a maritime forest. The western half is formed by an intertidal mud flat bordered to the south by sand dunes. Approximately thirty percent of the total area of the island is covered by salt marsh (Spartina alterniflora). Freshwater occurs naturally only after heavy rains, gathering in pools formed by dredge spoils. Normally the only other source of fresh water are holes dug and maintained by the horses. During the summer, these water holes are scarce and in the dry season, the water turns brackish (Hoffmann 1980). There are no other large herbivorous mammals found on the island. Foxes, as well as racoon tracks, were frequently seen. The island is uninhabited by man, who is the only 'natural' enemy of the studied horse population. Generally, the horses are rarely disturbed. Even tourists avoid the island because of its uninviting habitat. The climate is subtropical. The summers are hot and humid; the winters are correspondingly cool and humid.

POPULATION DATA

Origin of Horses

The population of horses studied originated from another feral horse population on adjacent Shackleford Island, one of the Outer Banks of North Carolina. Supposedly, the horses are descendants of shipwrecked Spanish mustangs (anonymous) of some 300 years ago. Both the studied horses, as well as the Shackleford ponies, resemble the Welsh and Norwegian ponies which reportedly were brought into North Carolina by Scottish settlers about 150 to 200 years ago. According to local sources, the horses on Shackleford have been feral since the 1880's, but are still rounded up and branded once a year. The horses on Bird Shoal-Carrot Island were occasionally looked after and provided with water during droughts since their transport to the island sometime in the 1930's until about 15 years ago. They have beem completely undisturbed ever since.


Pivers Isl.
4.0‰
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0 0.1 0.5 1 km
BIRD SHOAL - CARROT ISLAND
waterhole
salinity ‰
salt marsh
grass
dunes
maritime forest
intertidal sand and mudflats

Although almost all horses appeared to have intestinal parasites (Nematodes) at some time, none of them seemed to have been seriously affected. There were no other severe forms of illness, except for possibly one case. The horses showed special physiological adaptations to the unique environment. The horn of their hooves ruptured and spread out flat with increasing age, probably because they spent most of their lifetime standing in saltwater. They frequently drank brackish water and sometimes even sea water. They swam daily at any time of the year in intertidal creeks from their first day of life. The water temperature drops to 5°C in the winter months.

Social Organization

The social organization and population dynamics of the studied horse population did not differ from other feral horse populations. One to four mares and their offspring lived together year round in fairly stable harem groups dominated by one stallion. Over the study period, several two-male harem groups formed, with one dominant, driving, and reproducing male and one subdominant male at the group periphery. The breeding season, defined as the time span from the first parturition in the population until the last adult female estrus, lasted from mid-April until June or July. Thus, most foals were born within a four to six week range. At the age of one year, most yearlings left their maternal group. Two yearling females were bred and delivered successfully in their second year.

The population grew almost linearly from 24 horses observed in 1977 to 50 horses in 1982, with an average growth rate of 15.72 percent per year, versus a mortality rate of 4.6 percent per year (see Table 1). On the average, an adult mare had three foals in five years (fertility rate: .57 foals per year). The sex ratio of the population changed from roughly 1:1 in 1977 and 1978 to 1.4 males to 1 female in 1982.

Spatial Strategy

The harem groups maintained home ranges that varied seasonally and at times, overlapped to a large extent. In dry months, group encounters at commonly-used waterholes were frequent. Groups spent at least 12 percent of their total time watering (Hoffmann 1980). In most of these encounters, little agonistic behavior between stallions occurred. Newly-arriving groups usually waited 'in line', separated by their stallions, until access to the waterhole was free.

Grazing groups sometimes intermingled and later separated without any noticeable stallion interference or spatial competition, but generally groups showed certain preferences for

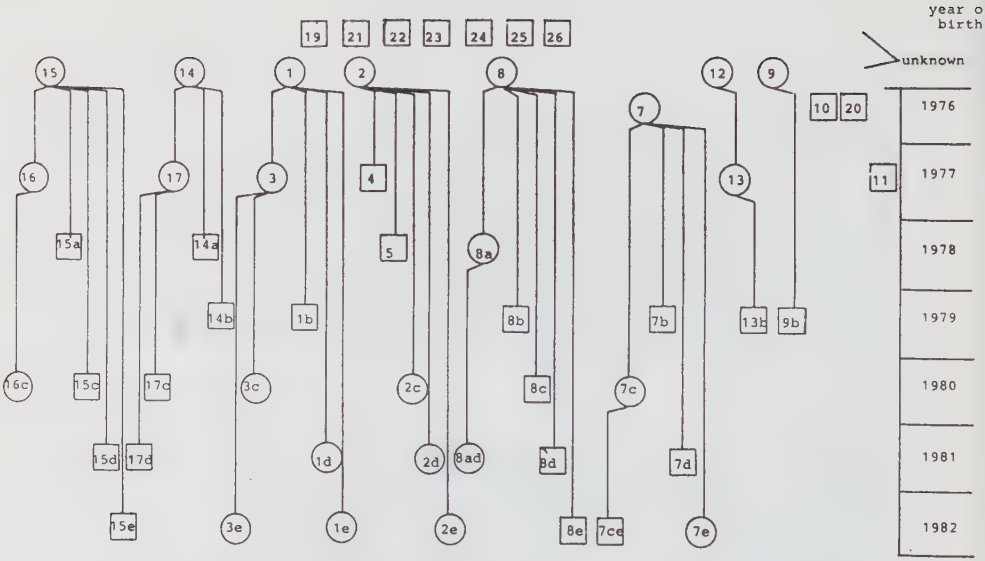


Fig.1) Geneaology of the horses on Bird Shoal-Carot Island; □ = males, ○ = females
All horses above the 1976-row were at least 2-3 years old when first sighted in 1977; several of the horses listed here died, and foals and adult animals which died and were not used for analysis are not listed here.

Tab.1) Population dynamics of all horses on Bird Shoal - Carrot Island

Year	Population Size		Sex Ratio		Fertility Rate	Mortality Rate		Population Size	
	Adult	Foal	Adult	Foal	Foal/adult Female/year	N dead	% of popul.	prior to next breeding season	popul. growth rate %
	♂ : ♀	♂ : ♀	♂ : ♀	♂ : ♀					
1976	9 : 8	3 : 1	1 : 1	3 : 1	?	?	?	20	20
1977	11 : 9	2 : 4	1.2 : 1	0.5 : 1	0.75	2	7.6	24	12
1978	11 : 13	4 : 1	0.8 : 1	4 : 1	0.55	2	6.9	27	12.5
1979	14 : 13	6 : 0	1.1 : 1	6 : 0	0.46	1	3	32	18
1980	20 : 12	3 : 4	1.6 : 1	0.75 : 1	0.53	-	-	39	21
1981	23 : 16	4 : 4	1.4 : 1	1 : 1	0.66	3	6.3	44	13
1982	27 : 17	3 : 5	1.43 : 1	0.6 : 1	0.50	1(foal)4 1		50	13.6
1976-1982					$\bar{F}$(1977-1982) =0.57±0.1	$\bar{d}$=4.6±2.8 (1977-1982)			$\bar{x}$=15.72

particular areas. Although territoriality was not observed, one group lived on one end of the island which it used exclusively throughout the study period. Territorial behavior was not observed in the stallion of this group.

Diet

The horses spent most of the time (75 percent in the winter, 56 percent in the summer) grazing on saltmarsh (Spartina alterniflora) (Hoffmann 1980, deWinter 1981, and Lin 1982), which is also true for other feral horse populations on the Outer Banks of North Carolina (Wood 1981). In the wintertime, Spartina patens was the second-most frequently grazed species, and in the summer, it was Strophostyles. Foals began to graze on Spartina alterniflora several days after birth. Based on studies on adjacent Shackleford Banks, the carrying capacity of saltmarsh for horses (two horses per hectare) had not been reached on Bird Shoal-Carrot Island in 1982 (0.5 horses per hectare).

METHOD

Observation Modus

Observations were conducted between sunrise and sunset with seasonal variations. In the summer, I observed in the morning and late afternoon to avoid the midday heat. (Pilot observations revealed that even horses became very inactive during the hot humid hours.) On harsh winter days, I generally observed from late morning until afternoon when the temperatures were above freezing. In order to gain enough observation hours, I observed on as many days as possible over the two-year period. I did not conduct night observations.

At the beginning of every observation day, the entire island was systematically scanned for horses. The location, identity, group composition, and activity was recorded for every individual. Individuals and groups were followed for as long as possible. This necessitated observations by boat (for example, in the flooded saltmarshes). The average observation distance was between five and twenty meters. The horses were obviously accustomed to my presence, since comparisons of short-distance observations with long-distance observations with field glasses or from behind trees did not reveal any differences in behavior.

After the population check, I returned to the individual or group to be observed. The location of every subject and its distance to every other horse in the vicinity (usually the group members) was noted every ten minutes. The frequency of every social behavior pattern, the partner of exchange,

and the response was continuously marked on prepared data sheets, usually for one observation hour. The social and environmental context was described and recorded. Durations of playing and grooming behavior were measured in five second intervals. Complex behavior was described by dictation. Behavioral observations were ended when the subject was no longer in sight.

Observation Time

From September 1980 until March 1981, all bachelors from one to five years of age were observed. From March 1981 until July 1982, all other horses on the island were included. Thus, all bachelors on the island were observed for two nonbreeding seasons (September 1980 through March 1981 and August 1981 through March 1982) and two breeding seasons (March 1981 through July 1981 and March 1982 through July 1982). All other animals were observed for the same two breeding seasons, but only one nonbreeding season (August 1981 through March 1982) was included. A total of 6,752.3 horse hours was spent on all horses on behavioral observations alone. Of this total, 4,253.4 hours were spent on male foals and bachelors, age 0 to 62 months (n = 22) (see Table 2a); 822.5 hours were spent on eight adult males (see Table 2b); 800.75 hours were spent on the 11 female foals and young females (see Table 2c); and 875.65 hours were spent on the 10 adult females (see Table 2d). The average frequency of observation hours varied in bachelors between 36.5 hours per animal (age 10 to 14 months) and 88.04 hours per animal (age 38 to 46 months). In all other animals, the average observation hours per animal per season did not vary to such an extent. The difference resulted from the different types of social organization. Young and adult females and adult males lived in stable groups, so observations distributed randomly over all groups led to roughly the same number of observation hours. However, bachelors lived singly or continually formed new associations. Thus, they were observed more frequently.

DATA ANALYSIS

Definition of Variables

Behavior Patterns

In order to measure the frequency of social behavior, I had to classify the events to be counted. I defined the smallest observable unit of behavior as a behavioral stereotype, such as 'ear position up', 'ear position half back', 'ear position flat back', 'sniff', 'stretch neck', 'turn', etc. A behavior pattern was defined as a single stereotype or (one and only one) combination of stereotypes. Every new combination of stereotypes, even if it occurred only once, was regarded as a behavior pattern.

Table 2a) Distribution of observation hours in male foals and bachelors (total 4253.4 h)

♂ age)** / ♂ elors	0-10 months	10-14 months	14-22 months	22-26 months	26-34 months	34-38 months	38-46 months	46-50 months	50-58 months	58-62 months
'e	17)*									
›e	35.25									
;e	9.25									
'd	36	40.75								
]d	27.75	27.75								
;d	75.75	47								
'd	42.25	48.25								
;c		28	84.25	79.75						
·c		26.5	96.25	71						
'c		40.75	30.25	48.65						
b				55.75	39	58.75				
b				22.5	43.5	43.25				
b			89	82	86.5	90.5				
b			92	82.5	83.5	68.5				
b			37.75	86.75	82.5	90				
b			50	208.25	115	74.25				
a					92.75	85	99	78.5		
a					69.25	48.5	74.5	71.75		
					113.5	71.75	113.5	33.75		
							83.5	106.5	52	42.25
							96.75	82.5	68.75	37.75
							61	74.5	62.75	44.75
hrs/horse)	45.43	36.5	68.5	70.79	80.27	70.05	88.04	74.58	61.16	41.58
	± 21.06	± 10.19	± 28.11	± 25.12	± 27.28	± 17.22	± 18.86	± 23.54	± 8.48	± 3.54
tal	243.25	255	479	637	725.5	630	528	447.5	183.5	124.75

)*: x is the number of hours spent on behavioural observation of the horse with the ID of the same row

)**: Immature indivduals were observed for 1,2,3 or 4 seasons, depending on their age; therfore the observation hours are compiled over age groups;

)***:The adult animal observation hours are given per season; the length of a season corresponds with the lengths of age periods in immature animals (see text).

Table 2b: Distribution of observation nours in adult males (total 822.5 h)

adult ♂ ID	BREED- 81 SEASON)***	NONBREED-81/82 SEASON	BREED- 82 SEASON
10	25.75	10	24.25
19	41.25	36.75	50
21	40.75	44.75	39.25
22	9	33.25	37.75
23	35.75	31.5	52
24	21	51.5	37
25	26.5	34	31.75
26	35.75	38.25	34.7
$\bar{x}$ (hrs/horse)	29.46	35	38.34
	± 11.07	± 12.08	± 9.10

Table 2c: Distribution of obs.hours in immature females (total:800.75)

foals (ID) *yearl.+ \ age)**	0-10	10-14	14-22	22-26
1e	11.5			
2e	24.25			
7e	31.25			
3e	18.75			
1d	63.25	39.75		
2d	50.5	39.00		
8ad	38.5	32.5		
2c		59	49.5	23.75
3c		26.5	34	43.5
7c		33	36.75	32.5
16c		25.25	49.5	38.25
$\bar{x}$ (hrs/horse)	34 ± 18.2	36.42 ± 11.38	42.43 ± 8.23	34.5 ± 8.45

Table 2d: Distr. of observation hours in adult females (total:875.65)

adult (ID) **	BREED 81)***	NONBREED 81/82	BREED 82
8a	26.5	34	31.75
3	26.5	34	31.75
25	36.5	43.75	41
1	27	37.5	37
2	27	37.5	36.25
8	25.25	10	24.25
16	25.25	10	dead
13	9	53.75	35.25
17	25.75	36.75	47.15
7	6.5	32.25	34.5
$\bar{x}$ (hrs/horse)	22.67 ± 7.91	32.95 ± 13.58	35.43 ± 6.36

Patterns with apparently common underlying meanings, stimuli, and results were grouped into one behavior category and labeled accordingly. For example, in the category, 'agonistic behavior', patterns were labeled as agonistic 3, agonistic 4, agonistic 5, etc. The intensity of the pattern as measured by the reaction of the opponent usually, but not always, increased with rising numbers. During the pilot study, all stereotypes and patterns occurring in the population were identified, recorded, and compared with the observations and descriptions in the literature (Antonius 1939, Grzimek 1944, Zeeb 1958, 1959, Trumler 1959, Feist 1971, Tyler 1972, Clutton-Brock 1976, and Wells and Goldschmidt-Rothschild 1978).

The following table presents the categories, labels, and patterns for the social behaviors found in this study.

Category	Label	Sequence of Stereotypes (Pattern)
Greeting	0	Ears up; naso-nasal contact
	1	Ears flat back; naso-nasal contact
Grooming	40	Ears up; initiating; allogrooming
	41	Ears up; initiating; mutual grooming
	42	Ears up; passive mutual grooming
Playing Behavior	39	Ears up; initiating
	42a	Ears up; snap; wrestle; groom
	6a	Ears up; chase
	9a	Ears up; bite
	10a	Ears up; front hoof beating
	11a	Ears up; front hoof beating; bite
	12a	Ears up; front hoof beating; bite; chase
Submissive Behavior	13	Ears flat back; stretch neck; teeth blecking
	14	Ears flat back; stretch neck; teeth clapping
	15	Ears up; walk away
	16	Ears flat back; run away
Agonistic Behavior	3	Ears flat back; (threat)
	4	Ears flat back; naso-nasal contact; head beating
	4b	Ears flat back; head beating-movement
	5	Ears flat back; naso-nasal contact; head beating; vocalization
	6	Ears flat back; chasing
	7	Ears flat back; snap
	8	Ears flat back; hindhoof kick; vocalization
	9	Ears flat back; bite
	10	Ears flat back; front hoof beating; vocalization
	11	Ears flat back; front hoof beating; bite; vocalization
	12	Ears flat back; front hoof beating; hindhoof kick; chase; vocalization

Defecation	20	Sniff
Marking	21	Sniff fresh pile
	25	Sniff old pile
	21b	Sniff fresh pile; defecate
	25b	Sniff old pile; defecate
	22	Sniff fresh pile; marking position
	26	Sniff old pile; marking position
	23	Sniff fresh pile; marking position; defecate
	27	Sniff old pile; marking position; defecate
	24	Sniff fresh pile; marking position; defecate; 180° turn; sniff own mark
	28	Sniff old pile; marking position; defecate; 180° turn; sniff own mark
Urine	37	Flehmen
Marking	29	Sniff urine
	33	Sniff urine; flehmen
	30	Sniff urine; marking position
	31	Sniff urine; marking position; urinate
	34	Sniff urine; marking position; urinate; flehmen
	32	Sniff urine; marking position; urinate; 180° turn; sniff own mark
	35	Sniff feces; flehmen
	38a	Sniff feces; marking position; urinate
	36	Sniff feces; flehmen; urinate
Driving	17	Ears flat back; stretch neck; chase
Behavior	18	Ears flat back; drive
Sexual	47	Ears flat back; sniff female
Behavior	48	Ears flat back; sniff female genitals
	51	Ears flat back; courting female; vocalization
	49	Ears up or flat back; mounting female
	50	Ears up or flat back; copulation with female

The stereotypes used in the list above are defined below.

drive -- chasing female with lowered head and stretched neck into a certain direction
marking position -- upright position with lifted tail
urine marking -- short blasts of urine onto the stimulus
defecation marking -- several 'units' of feces dropped onto the stimulus in marking position
flehmen -- olfactory investigation of strange stimulus with upper lip curled back and head extended into the air
vocalization -- any type of vocalization
head beating -- throwing the head back and up, simultaneously with the partner
wrestle -- both horses biting into the opponents hind legs while standing parallel and pushing him away in a circular movement
teeth blecking -- exposing the teeth of upper and lower jaw

teeth clapping -- exposing the teeth of upper and lower jaw, clapping the teeth together
initiating -- actively walking to another horse and establishing tactile contact.

Age Period

The occurrence and frequency of behavior patterns and categories were related to age. The age of bachelors and young females was expressed in time periods equivalent to the different seasons in the study. Therefore, the age periods used have two different lengths: (1) eight months (nonbreeding season) and (2) four months (breeding season). Smaller, arbitrarily chosen age periods (e.g. months) were not feasible in most cases because of the large total time scale to be considered (5 to 6 years in bachelors). Furthermore, the distribution of observation hours over time and the individual behavioral differences in horses are too large to yield any age correlated quantitative results on a scale smaller than chosen.

The data obtained from observations of horses of the same age, but in different seasons, were put together into the same age period. The table below is used as an example.

Example	Horse Identification 14b	15a
Observed in season:	age	age
Nonbreeding 1980	14-22 months	26-34 months
Breeding 1981	22-26 months	34-38 months
Nonbreeding 1981	26-34 months	38-46 months
Breeding 1982	34-38 months	46-50 months

(For the age period of 26-34 months, the data of horse 14b taken in the nonbreeding season of 1981 and the data of horse 15a taken in the nonbreeding season of 1980 were evaluated.)

Table 2 (pages 9 and 10) shows the number of horses observed in every age period (vertical column), their identification, and the number of seasons they were observed (horizontal rows). The data on adult horses were compiled in seasonal periods (the age of adult animals was not known) and were comparable to the bachelor and young female data respectively. In adult animals, the two breeding seasons were separated to discuss possible quantitative developments within the whole population over the observation period of two years.

In 1979 no female foals were born. Therefore, at the beginning of the female observation period in 1981, no two-year-old females (and in 1983, no three-year-old females) could be observed. Thus, I used only data on female foals and yearlings for the ontogenetic part of the project, assuming that four-year-old females were well into adulthood.

Social Context

I defined two different social contexts for the male horses. The two social contexts were: (1) permanent contact with females and (2) no permanent contact with females. The first context applied to (a) immature males (foals, yearlings, two-year-old males) who were members of the mother's harem group (These males were called foals and mothergroup bachelors respectively.); (b) sexually mature bachelors (age three to six years) which temporarily 'kept' mares but had not yet built up a stable harem group (These males are called harem group bachelors.); and (c) stallions with harem groups.

Frequency of Behavior

Every observed behavior pattern was counted as one event. The frequency of occurrence of every single pattern was standardized for every individual as the number of events per observation hour per age period (season). Thus, for every horse, the sum of all events of one pattern within one age period was divided by the number of observation hours for this horse.

The frequency of occurrence of a behavioral category was determined as the summarized frequency of occurrence of all patterns within this category. Again, this was standardized as events per hour per age period for every horse.

Absolute Frequency

The average absolute frequency of occurrence of a category was expressed as the arithmetic mean ($\bar{x}$) with standard deviation (s) of all individual events per hour in one age group for adult animals in one season.

Relative Frequency

The relative frequency was defined as the distribution of the absolute frequencies of every behavior category of an individual within one age period, expressed as the percent of the total social activity of this animal in this age period. The average relative frequency distribution was derived by calculating the mean of the individual relative frequencies of all horses of one age period with standard deviation. For this purpose all percent numbers were transferred into 'probits' with the angular transformation ($u = \arcsin p$, where p is a proportion from 0 to 1). The 'probits' were then retransferred into percent numbers. This procedure is necessary for doing statistical analysis on percent data. It prevents means ($\bar{x} \pm s$) from becomming larger than 100 or smaller than 0, but allows the application of statistical tests (Rohlf and Sokal 1982).

Horse Frequency

The horse frequency of a particular behavior pattern was defined as the number of horses per age period in which a certain behavior pattern occurred. This figure was calculated using the percent of all horses of this age period, independent of the actual occurrence of this pattern in every horse.

Absolute and Relative Variability

The absolute variability was determined as the total number of different behavior patterns observed to occur in the horses of a certain age period, independent of their actual frequency of occurrence. The relative variability was expressed by calculating the mean and standard deviation of the total number of different patterns occurring in every animal of one age period.

Distance Between Individuals

One way to determine whether an individual belonged to a group was to determine the average distance between this individual and the other individual(s) or group(s). The average distance between every group member and every other group member per observation hour (calculated from six measurements per individual per hour) was defined as the average intra-group distance. The individual distance (for example, between a foal and its mother) was always related to the average group distance at the same time. I used this procedure for two reasons. The actual distance in meters varied extensively between all animals depending on the group activity and the environmental situation. Secondly, this method seemed suitable for investigating whether a particular animal was closer to the group 'nucleus' (reproductive unit).

Statistical Tests

Initially, in order to state an expected frequency difference between two sets of data, the use of the t-test was planned. For paired data and for the distribution of variables, the paired t-test and the chi-square test was used, respectively. However, because the actual observed frequencies were, for most social behaviors and categories, extremely low, every application of a parametric test would have required a test for normal distribution. I am fairly safe to assume that some data sets were not normally distributed. Therefore, in those cases, I decided to use a non-parametric test.

With paired data, depending on the type of measurement and sample size, I applied the Sign test, Wilcoxon matched pair signed-rank test, or the Walsh test. Nonpaired data were analyzed with the Mann-Whitney U-test (Siegel 1956).

Rather than choosing a certain significance level for p, I decided to present the exact p-values, thus allowing for individual consideration of tendencies. I personally regard p-values between .1 and .05 as not significant. Under certain conditions though, I interpreted these values as revealing a tendency (see Results). P-values below .05 were regarded as significant.

RESULTS

Total Social Activity

The total frequency of the social activity in adult horses varied between 0.3 and 0.5 events per hour in mares and between 2 and 3 events per hour in stallions (Figure 2). In both sexes, social activity was lower in the nonbreeding season than in the breeding season (for females, $p \leq .05$; for males, $p \leq .01$, Wilcoxon).

The social activity of male foals increased during the first 14 months, but then decreased to the lowest value of the male socialization period at age 14 to 22 months. Young males then became increasingly more active reaching the adult male socialization level at the age of three years. The frequency distribution of the total social activity showed a strong seasonal character in immature males.

The frequency of social activities for the female foals and subadult females were within the range of adult females and not seasonal. Female foals showed less social activity than male foals of the same age (that is, 10 to 14 months, $p \leq .045$, Mann-Whitney U-test).

Absolute Frequency of Behavior Categories

Males (Figure 3, Table 3)

The most frequently observed social behavior category in stallions was agonistic behavior (0.74 to 1.3 events per hour per horse per season). This was followed by defecation marking (0.37 to 0.54 events per hour per horse per season) and driving (0.28 to 0.50 events per hour per horse per season). Together, these activities comprised roughly two-thirds of the total events. There was no significant difference observed in the frequency of these activities between the breeding and nonbreeding seasons. Sexual behavior and urine marking occurred significantly more often ($p \leq 0.017$, Mann-Whitney U-test) in the breeding season. In adult stallions, both playing and grooming behavior were the least observed social activities. Greeting was a frequently observed way of establishing contact, but only in the nonbreeding season.

A comparative examination of the frequency distribution over age in young males reveals at least three different maturation periods.

(1) Age 0 to 22 months. The frequency of the social activity was evenly distributed over the categories of grooming, play, greeting, and submission. Both forms of marking, as well as sexual behavior, appeared only sporadically. Driving was not observed at all. Except for during the first breeding season, agonistic behavior occurred less often than any of the nonagonistic and marking behaviors. The highest frequency of grooming at any age occurred in foals aged 0 to 10 months.

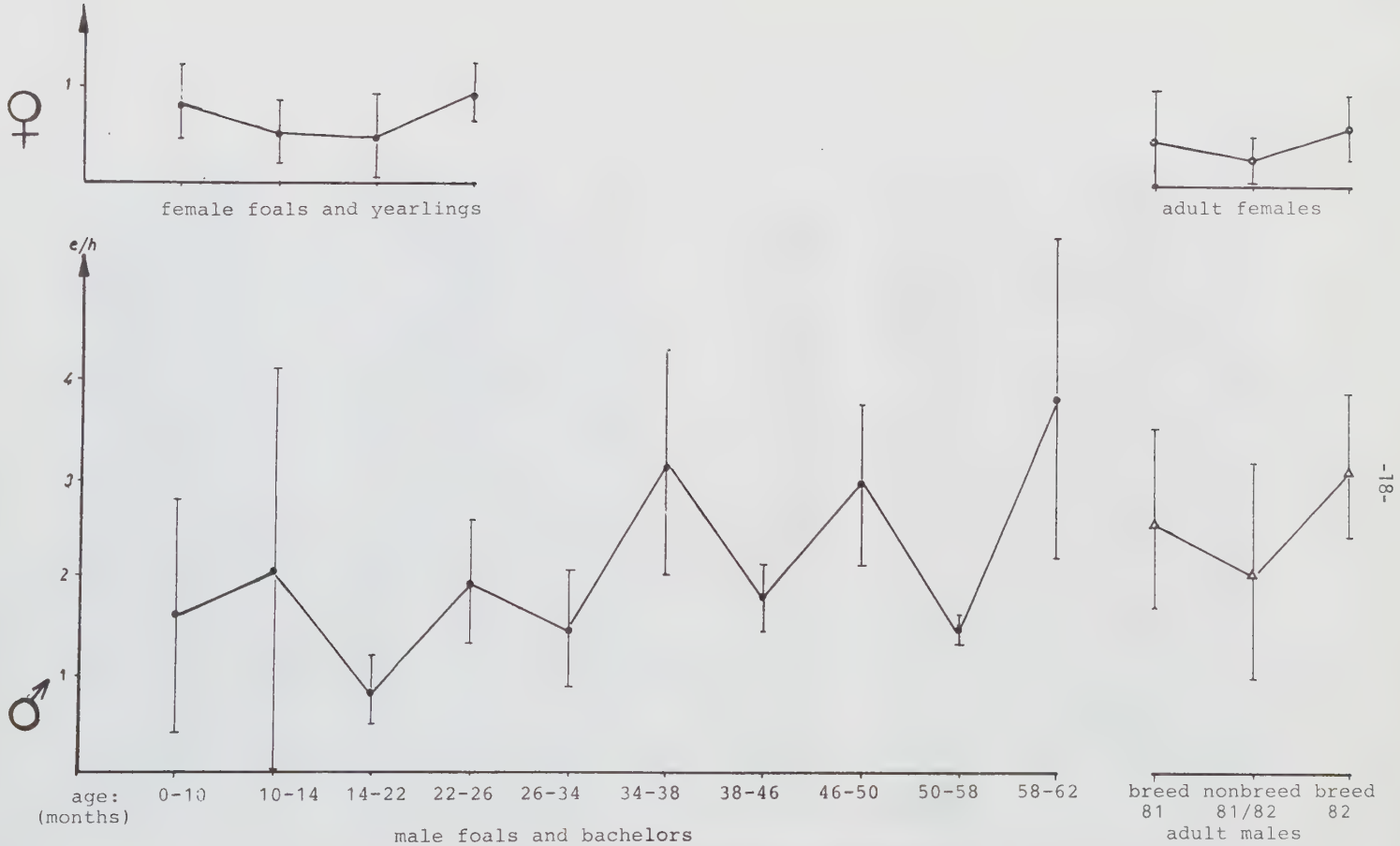


Fig.2) Total social activity per horse in different age periods: male foals and yearlings: •
(One value $\bar{x}+s_{\bar{x}}$ is the mean total frequency of the frequencies of all social behaviour patterns together, per horse in one age group (e/h/horse/age)) female foals and yearlings: •
adult males: △
adult females: ○

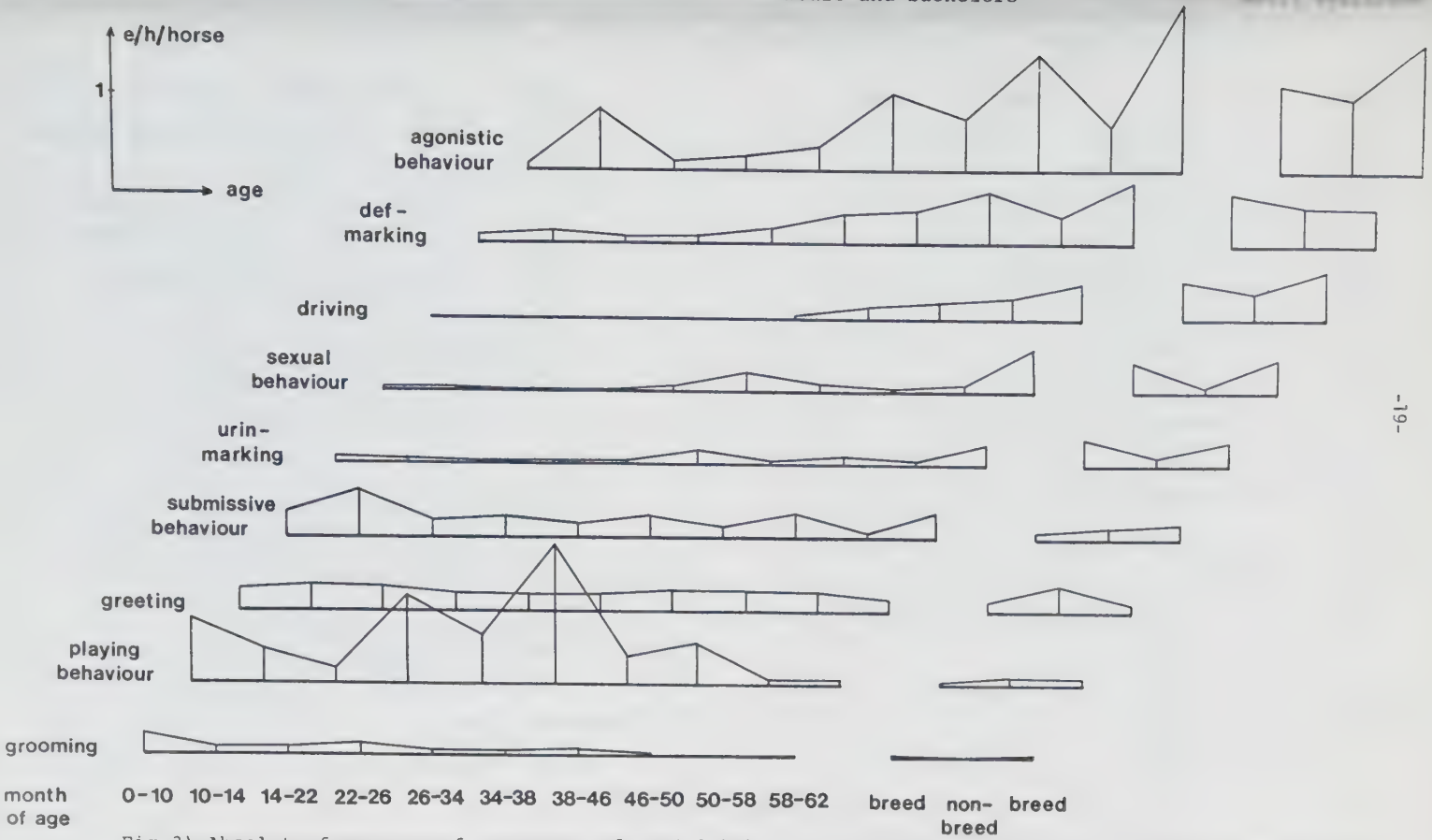


Fig.3) Absolute frequency of occurence of social behaviour categories in males in different age periods (foals and bachelors) and seasons (adult stallions). Exact values and standard deviation see Tab. 3

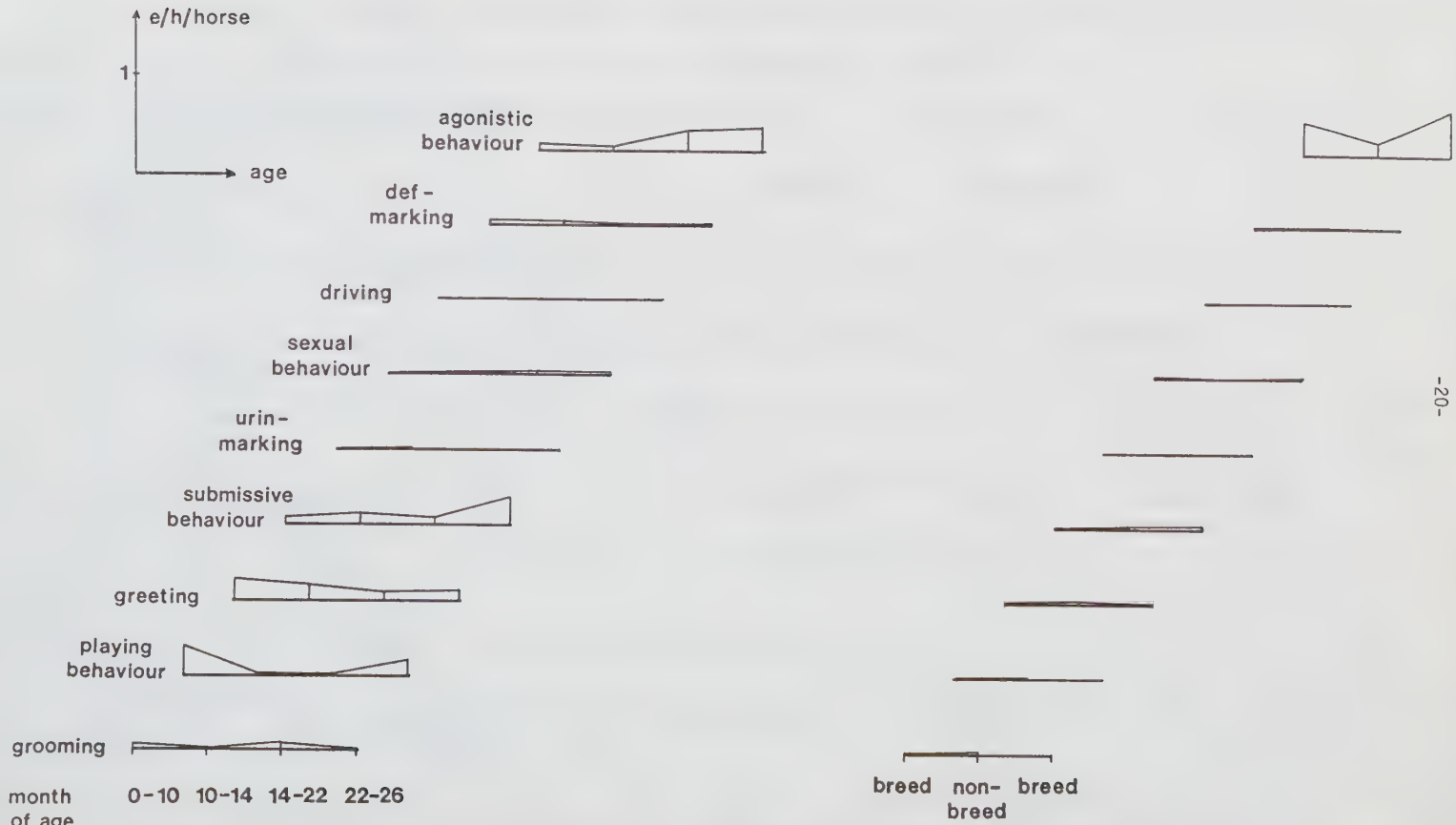


Fig.4) Absolute frequency of occurence of social behaviour categories in females in different age period (foals and yearlings) and seasons (adult females). Exact values and standard deviations see Tab.4)

ble 3) Absolute frequency or occurence of social behaviour categories in males
($\bar{x} \pm s_{\bar{x}}$ = mean observed frequency of occurence/obs.hr of all behaviour patterns of the given behaviour category per horse of this age period)

haviour tegories: \ age:	0-10 month	10-14 month	14-22 month	22-26 month	26-34 month	34-38 month	38-46 month	46-50 month	50-58 month	58-67 month	Saisons: breed81	non-breed82	breed82
gonistic ehaviour	.074 ±.08	.618 ±.89	.105 ±.10	.148 ±.10	.246 ±.13	.774 ±.56	.53 ±.22	1.18 ±.46	.454 ±.07	1.68 ±.92	.874 ±.58	.743 ±.46	1.30 ±.54
ef.- marking	.093 ±.09	.131 ±.12	.076 ±.05	.086 ±.09	.167 ±.08	.301 ±.24	.3408 ±.18	.536 ±.19	.273 ±.08	.635 ±.21	.544 ±.29	.40 ±.14	.37 ±.15
driving	-	-	-	-	-	.024 ±.07	.122 ±.16	.171 ±.36	.223 ±.10	.385 ±.28	.396 ±.50	.28 ±.29	.50 ±.29
sexual ehaviour	.030 ±.07	.039 ±.09	.0039 ±.006	.008 ±.02	.0497 ±.08	.195 ±.35	.086 ±.07	.0375 ±.06	.088 ±.86	.445 ±.35	.311 ±.60	.055 ±.079	.35 ±.36
urin marking	.0594 ±.07	.0421 ±.09	.0162 ±.02	.0264 ±.025	.0195 ±.04	.1457 ±.09	.023 ±.024	.0902 ±.05	.0571 ±.03	.213 ±.023	.284 ±.218	.096 ±.06	.253 ±.193
ubmissive ehavior	.265 ±.45	.4957 ±.73	.1781 ±.076	.230 ±.12	.1422 ±.07	.2411 ±.15	.123 ±.05	.2524 ±.159	.0529 ±.076	.27 ±.29	.0588 ±.0938	.109 ±.18	.175 ±.18
greeting	.226 ±.23	.267 ±.19	.245 ±.15	.184 ±.096	.217 ±.17	.1838 ±.08	.227 ±.095	.228 ±.14	.2117 ±.10	.135 ±.06	.1 ±.1	.227 ±.27	.077 ±.07
lay- ehavior	.653 ±.55	.356 ±.53	.150 ±.07	1.14 ±.46	.509 ±.42	1.47 ±.40	.297 ±.25	.44 ±.36	.044 ±.044	.051 ±.045	.014 ±.029	.0947 ±.08	.071 ±.08
grooming	.20 ±.3	.72 ±.13	.088 ±.06	.120 ±.08	.049 ±.05	.058 ±.098	.072 ±.063	.024 ±.035	-	-	.0293 ±.036	-	.022 ±.023
	foals and bachelors										adult stallions		

Table 4) Absolute frequency of occurence of social behaviour categories in females
($\bar{x}$ & $s_{\bar{x}}$ = see Table 3)

behaviour categories: \ age	0-10 month	10-14 month	14-22 month	22-26 month	Saisons: breed 81	non-breed 82	breed 82
agonistic behaviour	.064 ±.06	.057 ±.04	.2209 ±.26	.253 ±.143	.35 ±.44	.144 ±.18	.466 ±.28
def.- marking	.064 ±.03	.046 ±.053	.016 ±.019	.01 ±.02	.02 ±.06	.0178 ±.031	.001 ±.005
sexual behaviour	.005 ±.01	.014 ±.018	.033 ±.05	.025 ±.04	.019 ±.04	-	.0106 ±.03
urin marking	.007 ±.01	.017 ±.02	-	-	-	-	-
submissive behaviour	.096 ±.08	.137 ±.13	.087 ±.054	.301 ±.322	.012 ±.029	.033 ±.06	.0439 ±.048
greeting	.220 ±.10	.172 ±.16	.084 ±.12	.1138 ±.115	.0208 ±.046	.047 ±.06	.031 ±.02
play- behaviour	.31 ±.20	.030 ±.033	.022 ±.019	.166 ±.28	.005 ±.01	.0035 ±.01	-
grooming	.066 ±.097	.031 ±.05	.083 ±.129	.0138 ±.027	.0225 ±.03	.0424 ±.05	-
	foal and yearling females				adult females		

(2) Age 22 to 38 months. At this age, just before reaching sexual maturity, playing behavior was by far the most frequently observed social behavior in young males. The frequency of grooming and submission decreased with age, whereas the frequency of marking, agonistic behavior and sexual activity began to increase slowly. Driving occurred first after sexual maturity (26 to 38 months).

(3) Age 38 to 62 months. Between the 38th and 62nd month of life, the whole set of behavior categories gradually shifted into the adult male frequency distribution type. Frequencies of nonagonistic categories (such as play behavior, grooming, and greeting) continuously decreased, whereas behavior patterns of the other categories were used more frequently. Bachelors trying to build up their own harem group (age 46 to 50 months) for the first time used significantly more agonistic and submissive behavior than adult stallions ($p \leq .031$, Mann-Whitney U-test, for agonistic behavior and $p \leq .045$, Mann-Whitney U-test for submissive behavior). At the same age, the bachelors played more than adult stallions.

Generally, agonistic and submissive behavior, and after maturity, urine marking, were observed more often in the breeding season than in the nonbreeding season. Playing behavior showed strong seasonality only during its peak frequency (age 22 to 38 months). The development of all other behavior categories in bachelors was seasonally independent. In adult stallions, sexual behavior, urine marking, and to some extent, driving, appeared more often in the breeding season.

Females (Figure 4, Table 4)

In adult females, only agonistic behavior was observed to occur frequently (0.14 to 0.46 events per hour per horse per season). All other categories of behavior either did not appear at all during the observation period (for example, driving or urine marking) or occurred very infrequently (up to 0.04 events per hour per horse per season). Grooming and playing behavior occurred only in two seasons.

In female foals and yearlings, all categories were observed except driving. In male as well as in female foals (age 0 to 10 months), social activities were relatively evenly distributed over the categories playing behavior, greeting, and submission. Agonistic behavior and grooming were observed less frequently, and urine marking and sexual behavior were observed hardly at all. Between their first (10 to 14 months) and second (22 to 26 months) breeding season, female yearlings showed an increase in the frequency of agonistic and submissive behaviors, whereas the frequencies of urine marking, playing behavior and greeting decreased. At the age of 22 to 26 months, young females (being sexually mature and reproductive) showed a frequency distribution of categories quite different from that of adult mares and more similar to that of males of their same age.

A comparative view of male and female frequencies and their distirubtions shows that in foals (age 0 to 10 months), there was no significant difference between both sexes except for urine marking. In male foals, urine marking occurred significantly more often than in female foals ($p \leq .042$, Mann-Whitney U-test). Only after the age of 10 months did the frequency of the various behavior categories in yearlings and subadult males become and remain significantly higher than in females of the same age group (10 to 14 months: defecation marking, $p \leq .023$; 14 to 22 months: grooming, $p \leq .019$; playing, $p \leq .0004$; submission, $p \leq .03$; Mann-Whitney U-test). This was also partly true for male yearlings that stayed in their group until the age of 22 to 26 months. They played and groomed significantly more than females of the same age (playing behavior, $p \leq .014$; grooming, $p \leq .039$; Mann-Whitney U-test).

Resting and Nursing (Figure 5)

One of the most frequently observed activities in horses was resting (Figure 5a). Resting comprised approximately 10 percent of the total observation time among adults in the winter and up to 20 percent of the time in the summer. There was no significant difference in the amount of time spent in resting between adult males and females, although the mean values for females were higher than the mean values for males. Male and female foals rested between 40 percent and 50 percent of the observed time during their first two months of life. In the following months, the frequency of resting decreased and reached the adult level during the first breeding season. Female foals tended to rest more than male foals ($p \leq .079$, Mann-Whitney U-test), as did the one-year-old ($p \leq .01$, Mann-Whitney U-test), and two-year-old females ($p \leq .01$, Mann-Whitney U-test). Resting frequencies of bachelors showed no seasonal variation until they became permanently attached to harem groups (age 50 to 58 months).

The frequency of nursing of foals (Figure 5b) decreased from 1.24 events per hour (male) and 1.50 events per hour (female) in their first two months of life. By the time of their first breeding season, the nursing frequencies were .025 events per hour (male) and .07 events per hour (females). Most of the foals were weaned by this time, and only in a very few horses was nursing observed until the age of 1½ years.

Relative Frequency of Behavior Categories

Every animal at a certain age had its own specific distribution of behavior categories within its total social activity. The mean distributions over age are compared between the different types of bachelors. (Note: Mothergroup bachelors and 'real' bachelors of the same age are different individuals.) Bachelors who had left their group never returned to their or any harem group until they were sexually mature. After sexual maturity,

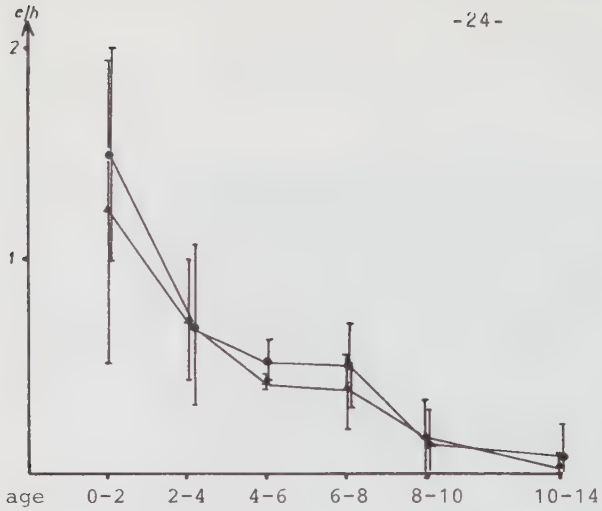


Fig.5b) Mean frequency of nursing bouts / horse / age period of male (▲) and female (o) foals

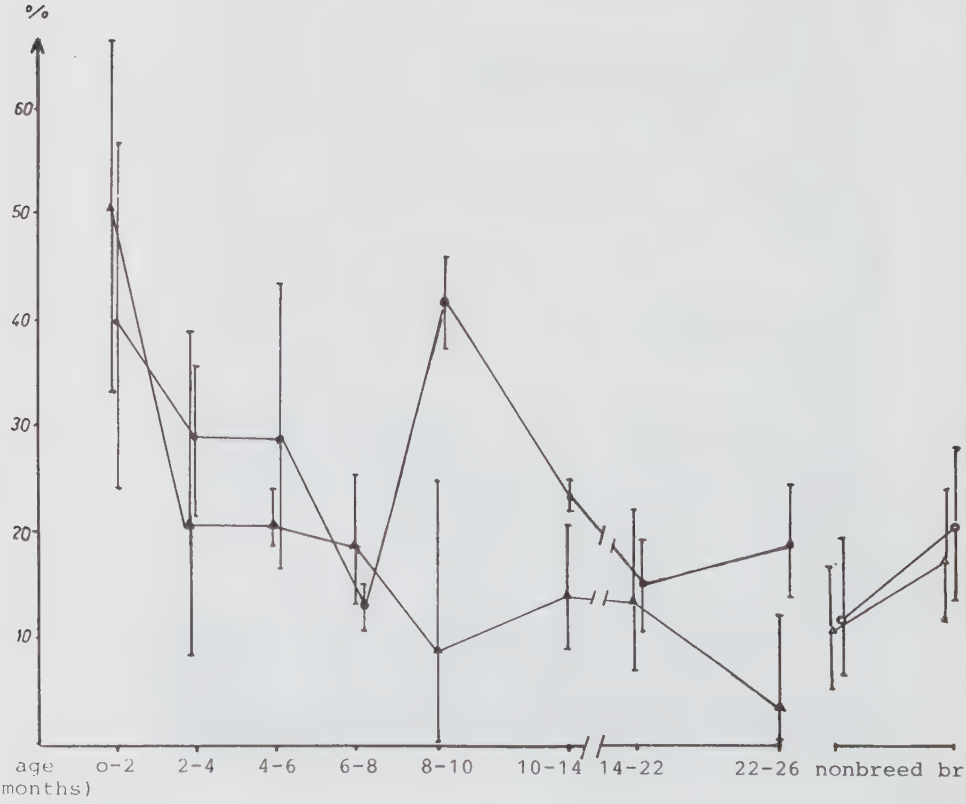


Fig.5a) Mean time spent on resting / horse /age period of male (▲) and female (●) foals and yearlings and adult stallions (△) and mares (O) in % of obs.hours

bachelors try more and more successfully to keep females. Thus, the social events of these mature bachelors were evaluated partly as bachelor values and partly as harem group bachelor values, depending on their social environment.

Agonistic and Submissive Behavior (Figure 6a and 6b)

Male foals which had left their mothergroup at the age of 10 to 14 months spent a significantly higher amount of their social activity on agonistic behavior ($p \leq .025$, Mann-Whitney U-test) and submissive behavior than male foals remaining in their mothergroup. These two behaviors accounted for 90 percent of the total social activity in foals that had left the mothergroup, whereas foals remaining in their mothergroup spent only 20 percent of their time on these two social activities. During the age periods of 22 to 26 months and 26 to 34 months, the situation was reversed. Mothergroup bachelors were relatively more submissive than bachelors at the age of 22 to 26 months, and significantly more aggressive during the nonbreeding season at 26 to 34 months ($p \leq .072$, Mann-Whitney U-test). Sexually mature bachelors in association with females spent a higher percentage of their social activity on agonistic encounters ($p \leq .07$, Sign test) and significantly less on submissive behavior ($p \leq .019$, Sign test) than when they were just bachelors. In adult stallions, the correlation between female presence and relative frequency of agonistic behavior was reversed. Stallions which had lost their group spent a higher proportion of their total activity on both agonistic and submissive behaviors than harem group stallions.

Defecation Marking and Urine Marking (Figures 6c and 6d)

The relative frequency of defecation marking in young males increased with age, but there was no context-related frequency changes. In harem group bachelors, the distribution pattern of defecation marking over age was not seasonal. The relative frequency peaked at 46 to 50 months, and then declined to the adult male values.

Urine marking hardly occurred at all in bachelors, and thus, it filled only a small part of their social 'budget'. Only in sexually mature bachelors with permanent contact with females did urine marking become a frequently used activity. While being a bachelor, the same horse showed no urine marking at all.

In adult horses, both the relative frequency distribution of urine marking and defecation marking resembled the harem group bachelor distribution. There was no context-related differences in defecation marking between stallions and males having lost their harem group and the latter performed hardly any urine marking when compared with harem group stallions.

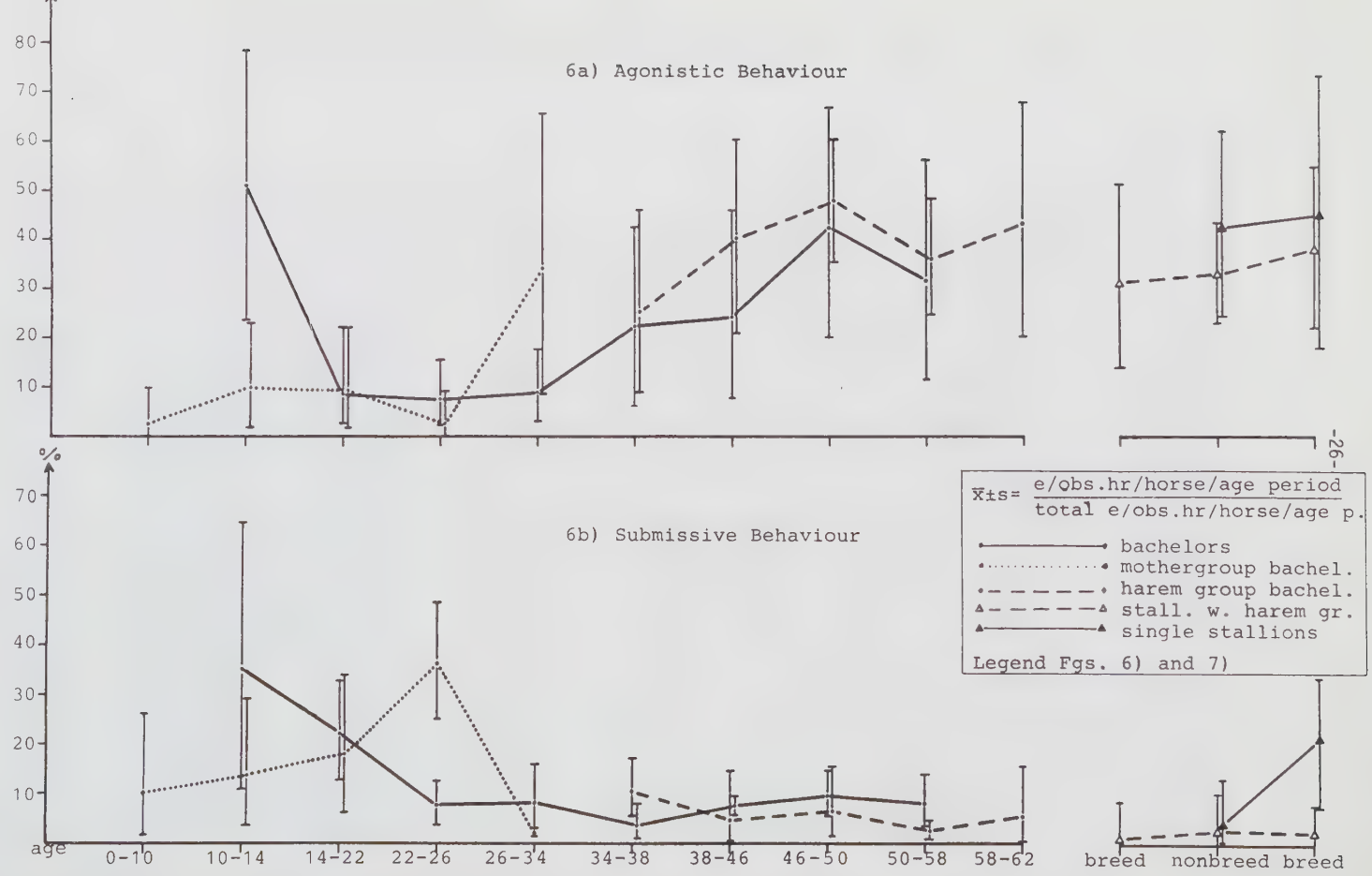


Fig.6) Relative frequency distribution of behaviour categories, within one age group, over age in males

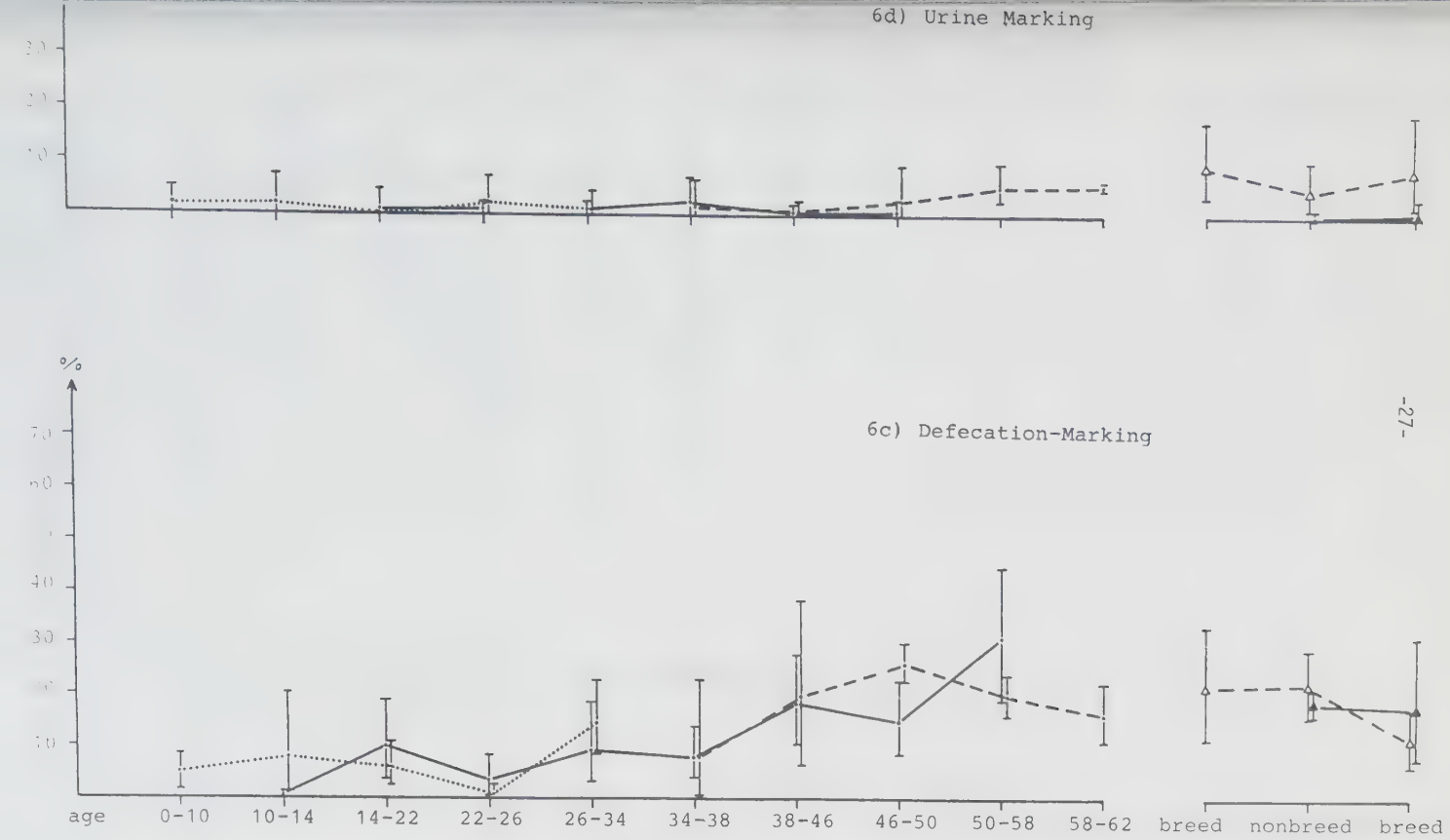
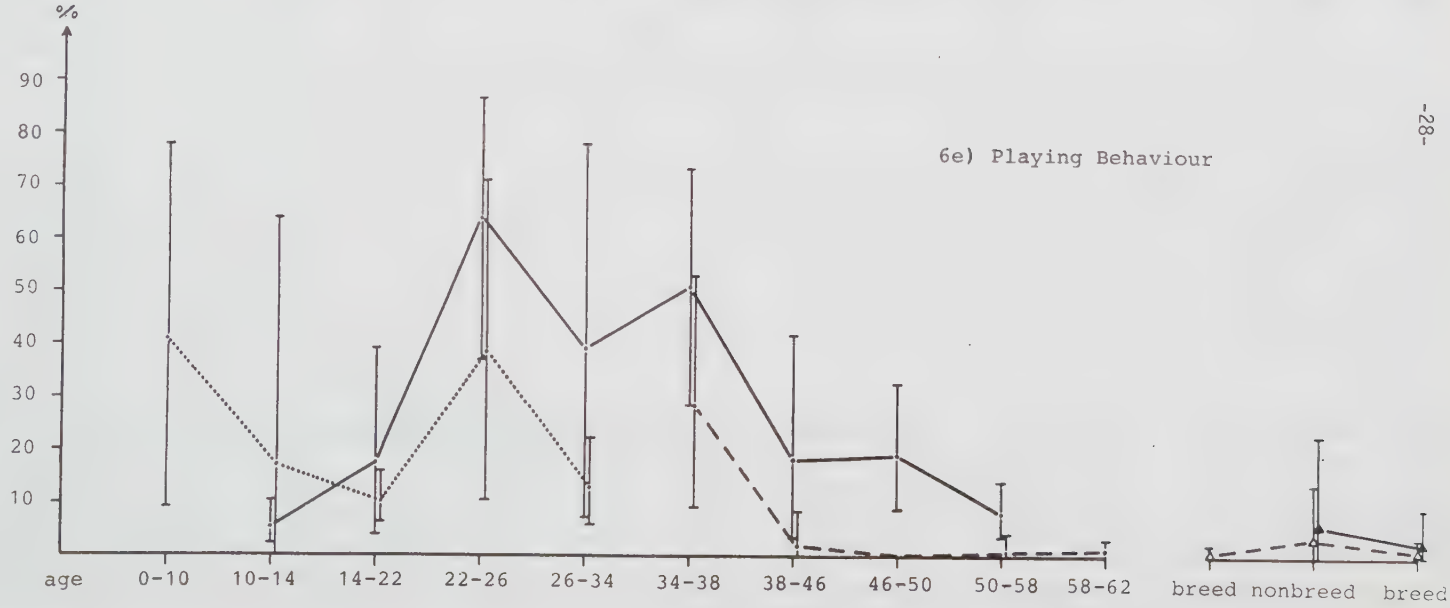
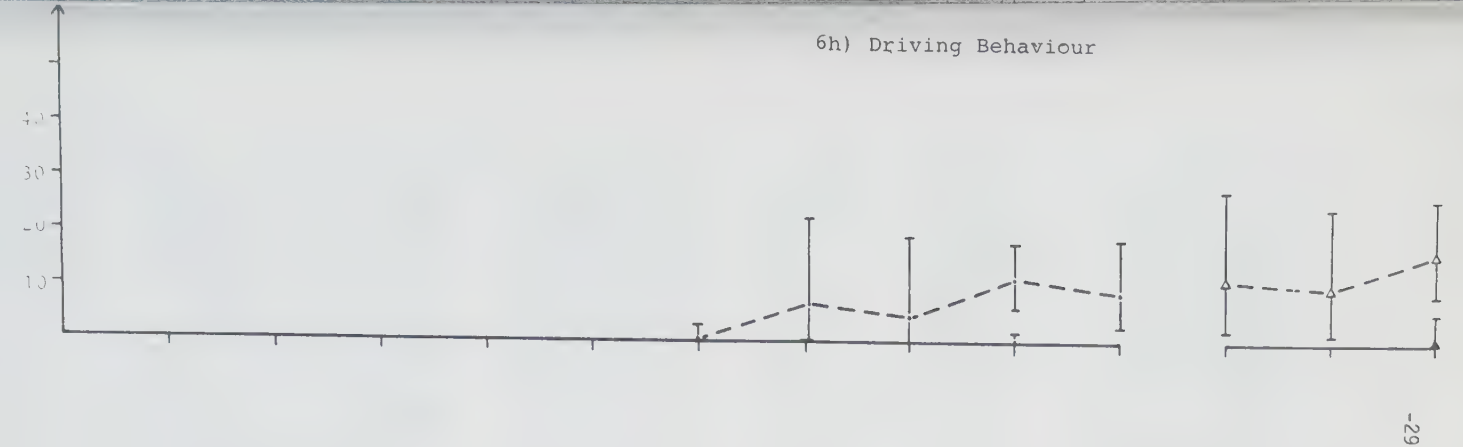


Fig.6) Relative frequency distribution of behaviour categories in males (legend see Fig.6b)

6f) Grooming Behaviour



6e) Playing Behaviour



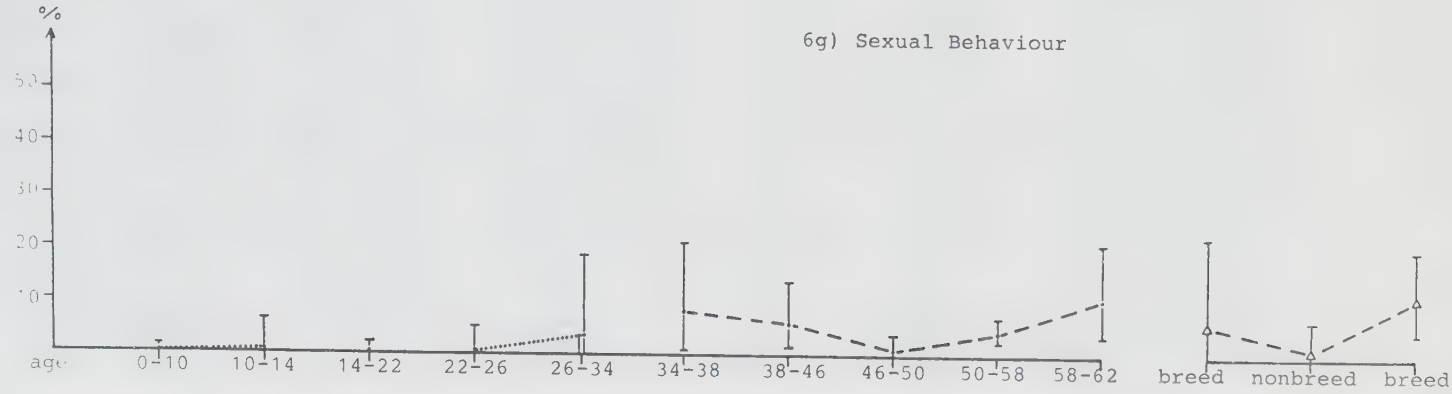


Fig.6) Relative frequency distribution of behaviour categories in males (legend see Fig.6b)

Playing Behavior (Figure 6e)

Playing behavior comprised up to 60 percent of the social behavior in bachelors and was strongly context dependent in its relative frequency. Mothergroup bachelors spent significantly less of their social activities on play than did bachelors of the same age (14 to 22 months, $p \leq .017$; 22 to 26 months and 26 to 34 months, $p \leq .07$; Mann-Whitney U-test). Males at the age of 46 to 50 months did not play at all when being a harem group bachelor, but did spend about 18 percent of their social activity on play as 'real' bachelors.

Grooming Behavior (Figure 6f)

The relative grooming frequency in young bachelors was not different from the frequency found in mothergroup bachelors. Harem group bachelors spent less of their social activity on grooming than did bachelors. Neither adult bachelors nor old bachelors of any status groomed.

Driving and Sexual Behavior (Figures 6g and 6h)

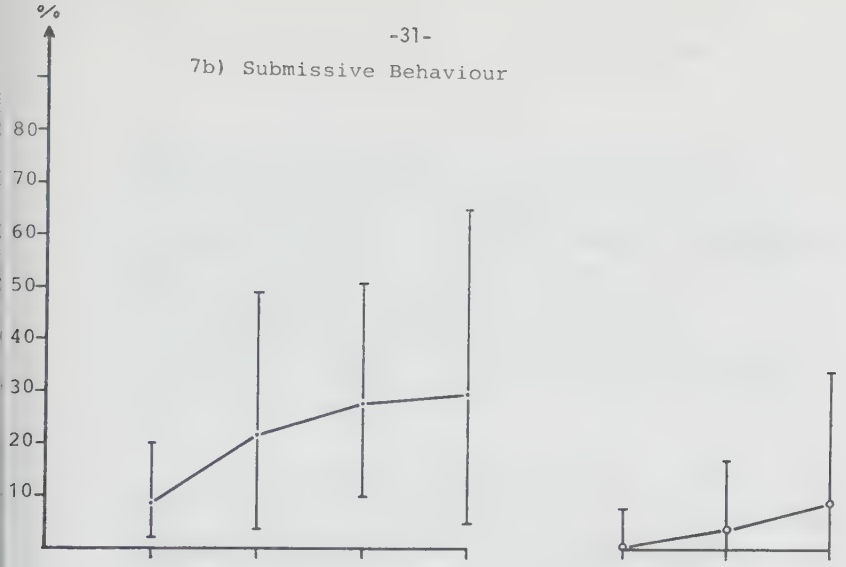
The relative frequency of both driving and sexual behavior were strongly context dependent. Driving occurred only in sexually mature males and furthermore, they only drove females when they 'possessed' one. Passing females of other groups were not driven.

The same context dependency was true for sexual behavior. Bachelors with permanent associations with adult females showed sexual behavior. No sexual activity was directed against temporarily contacted females, except for yearling estrous fillies. Two-year-old mothergroup bachelors did show some sexual behavior, which at the age of 26 to 34 months actually represented approximately 5 percent of their social activity (just as in adult males). In adult stallions, the relative frequency of sexual behavior was strongly seasonal. Driving had almost no seasonal character.

In adult females, between 40 percent (nonbreeding season) and 80 percent (breeding season) of their social activity had agonistic character (Figure 7a). Submissive and grooming behavior accounted for 2 to 10 percent of their social activity (Figures 7b and 7c, respectively). All other categories of behavior took only a minimal part of the female social activity or did not occur at all (Figures 7d and 7f).

In immature females, the relative frequency of both agonistic and submissive behavior was very low in foals aged 0 to 10 months, but continuously grew with age. At age 22 to 26 months, these behaviors together comprised almost 60 percent of their social activity (Figures 7a and 7b). A much larger portion of the young females' social behavior has a submissive

7b) Submissive Behaviour



7a) Agonistic Behaviour

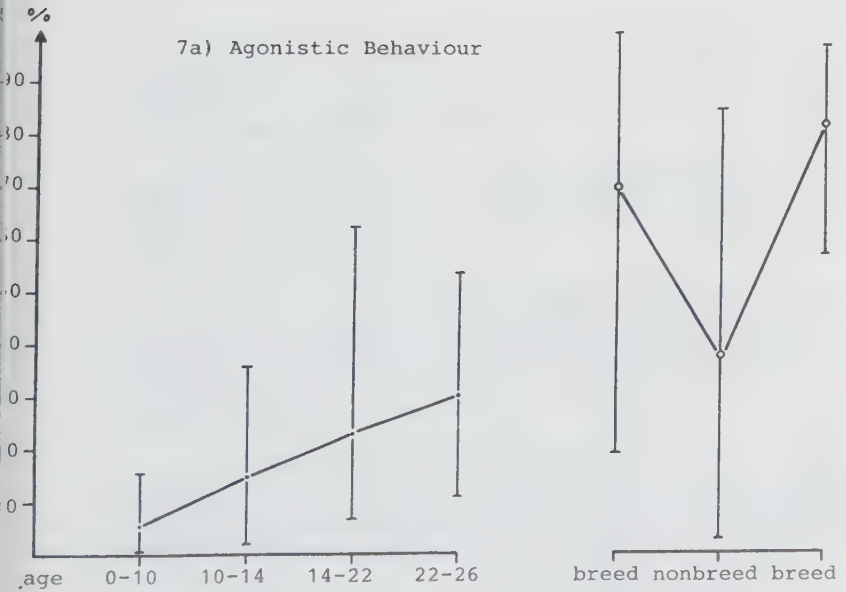


Fig.7) Relative frequency distribution of behaviour categories, within one age group, over age in females

o = adult females, • = immature females

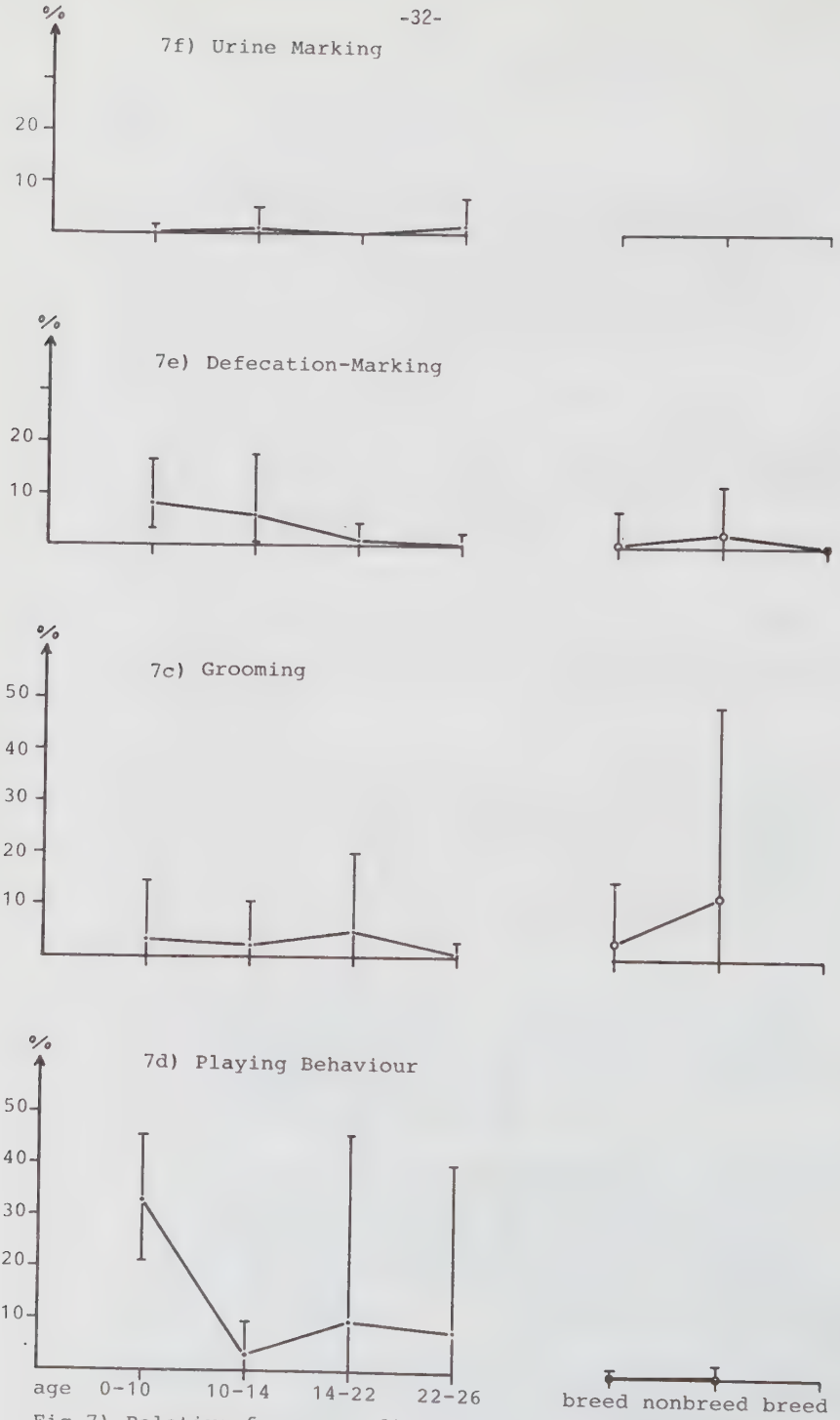


Fig.7) Relative frequency distribution in females

character and a much smaller part had an agonistic character than was apparent in the adult female distribution. The relative frequencies of both defecation marking and urine marking (the latter occurring only in immature females) decreased with age (Figures 7e and 7f). The relative frequency of playing behavior (Figure 7d) also decreased with age. In female foals, playing was the most heavily practiced social activity (30 percent). Grooming, which comprised only 3 to 4 percent of the social activity of young females (Figure 7e) did not show any development in its relative frequency distribution over age. In adult females, grooming was a very infrequent part of the social activity, and in the last season, playing did not occur at all.

In general, there was no difference in the relative frequency distribution between male and female foals. Only after their first breeding season did female yearlings spend a significantly larger proportion of their time on agonistic and submissive behavior than male yearlings in bachelor status ($p \leq .06$, Mann-Whitney U-test) and mothergroup bachelors. The female yearlings spent significantly less of their time on marking ($p \leq .025$, Mann-Whitney U-test), and grooming ($p \leq .013$, Mann-Whitney U-test), and playing behavior ($p \leq .013$, Mann-Whitney U-test). In young, as well as in adult, females, the standard deviations from the mean were much larger than in males, indicating a larger individual variation in the relative frequency distribution between females than between males.

Completion of Behavior Set

The behavior set was defined as the total number of different behavior patterns found in all animals on the island, independent of their frequency of occurrence. In males, a total of 59 different social behavior patterns was observed. Thirty-three of these occurred in females also.

In male foals (age 0 to 10 months), I observed 30 different behavior patterns. Between the first and third year of life, this number steadily increased to 58. At the age of 38 to 46 months, all behavior patterns found on the island had occurred at least once in males (Figure 8a).

In general, the period of completion can be divided into three parts: (1) the foal period, with the highest number of new patterns occurring, (2) the young bachelor period (14 to 22 months), with the lowest number of new behavior patterns, and (3) the 22 to 38 month range, with an average of six new behavior patterns per season.

In females, the development of the behavior set was quite different (Figure 9a). Female foals developed 23 out of a total of 33 female-specific patterns by ten months. The behavior set was slowly completed by the age of 34 to 38 months. The increase in completion appeared to be seasonally independent in both sexes.

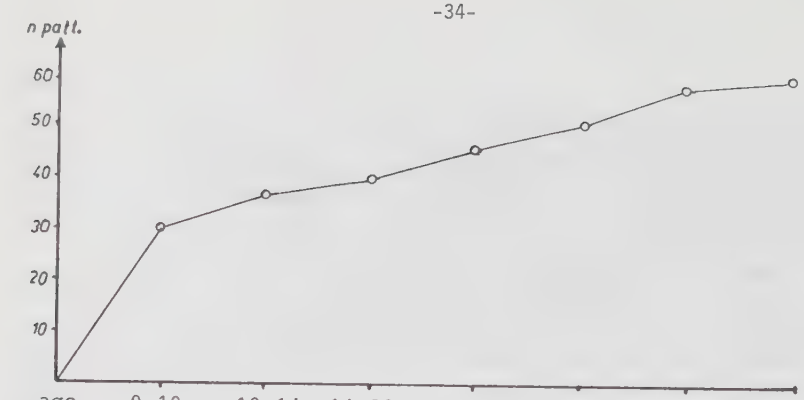


Fig.8a) Completion of behaviour set in juvenile males
(o)=n new patterns occuring in the pop. + previous new patt

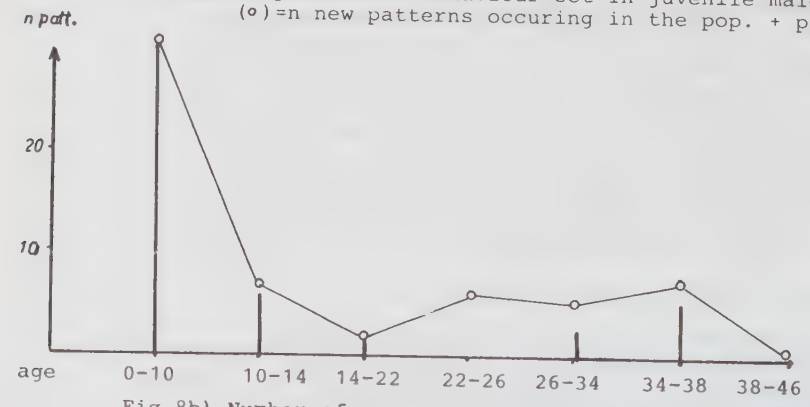


Fig.8b) Number of new patterns occuring first (o) in males;
of these occuring in contact with females (|).

Fig.8c) Age period in which the given category was completed
(all patterns of this cat. had occured at least once in
the population) in males

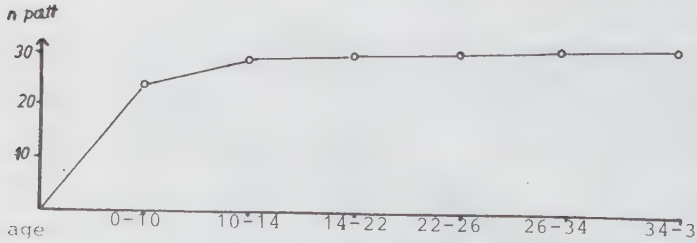


Fig.9a) Completion of behaviour set in juvenile females

Although both the total activity as well as some behavior categories had a seasonally-dependent frequency, the appearance of new behavior patterns increased steadily with age. The largest number of new behavior patterns in males was observed to occur in contact with females, except for males aged 22 to 26 months (Figure 8b).

A comparative view of male and female completion patterns reveals that female foals had shown almost 75 percent of the number of behavior patterns typical for their adulthood at the age of 10 months, whereas males at that age had shown only 50 percent of their adult patterns. Thus, the females completed their set faster and earlier in life than the males.

The sequence of the completion of the various behavior categories reveals that nonagonistic, friendly social categories were completed earlier in life than categories with patterns of a competitive character (Figure 8c). (A category was completed when all patterns in this category had occurred.) Grooming and greeting were completely represented in foals, followed by submission, and at the age of 22 to 26 months, playing behavior. Agonistic behavior, defecation marking, urine marking, and driving were not completed before sexual maturity (34 to 38 months). The complete set of sexual behavior did not appear before the age of 38 to 46 months.

Absolute and Relative Variability of Patterns

The previously presented behavior set could also be regarded as the potential behavioral variability on the population level for both males and females. However, there were no horses which in any given season showed all the behavior patterns that had been observed to occur in their sex on the island. Furthermore, there were no age periods or seasons in which I observed all behavior patterns occurring. Therefore, in order to gain some understanding of the behavioral flexibility of the adult animals in this population, it seemed appropriate to investigate the absolute variability and relative variability and to compare them over age and sex.

If the horses of a certain age period used the same number, but different types of behavior patterns, then their individual flexibility (relative variability) was smaller than the age-period specific flexibility (absolute variability). A possible difference in absolute and relative variability would thus lead to the assumption that horses do have an individually differing set of behavior patterns. This in turn would lead to a larger variability within a certain age group than in any of the individuals' variability.

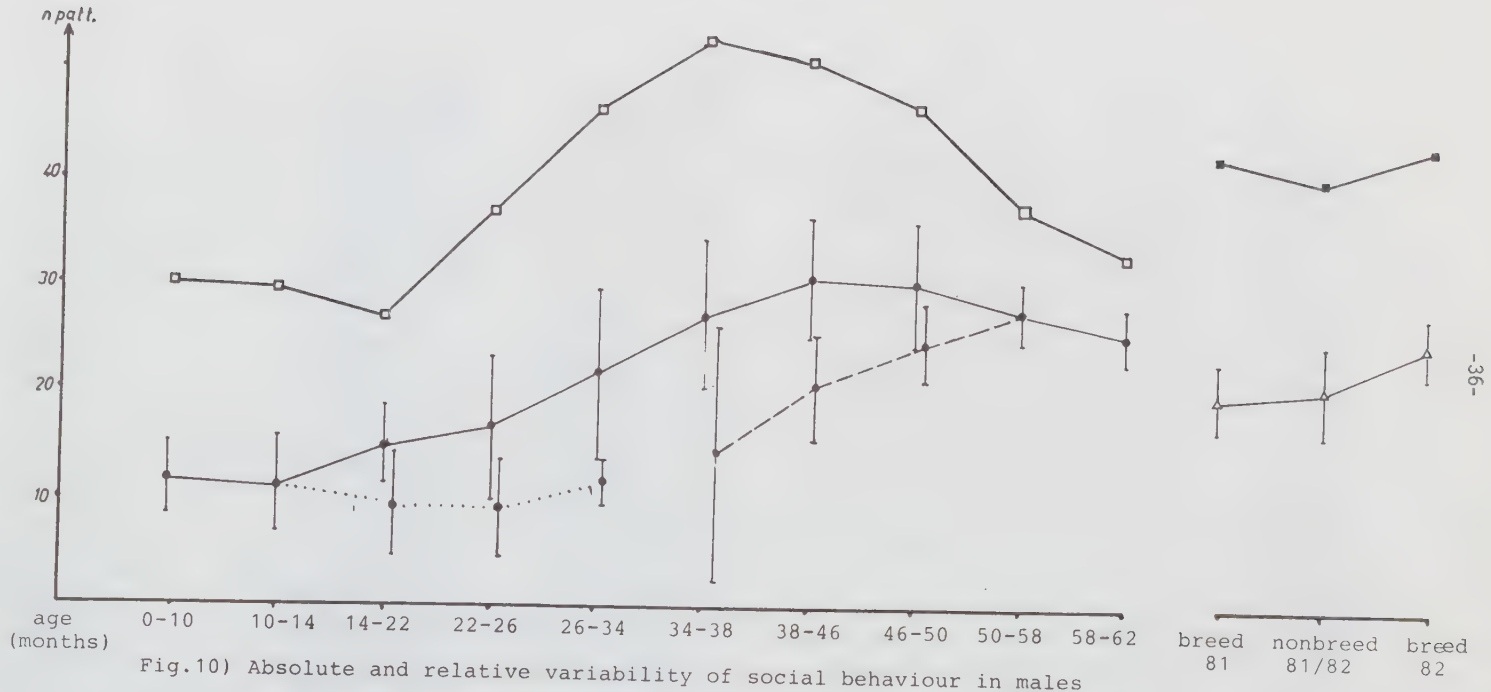


Fig.10) Absolute and relative variability of social behaviour in males

absolute variability: total number of different patterns used / age, in Stallions / season
(□) = abs. var. of foals and bachelors, (■) = abs. var. of stallions

relative variability: mean of no. of diff. patterns used in one age period by 1 horse ($\bar{x} \pm s_{\bar{x}}$)
(●—●) = bachelors; (●···●) = mothergroup bachelors; (●-·-●) = harem group bach
(▲—▲) = adult stallions

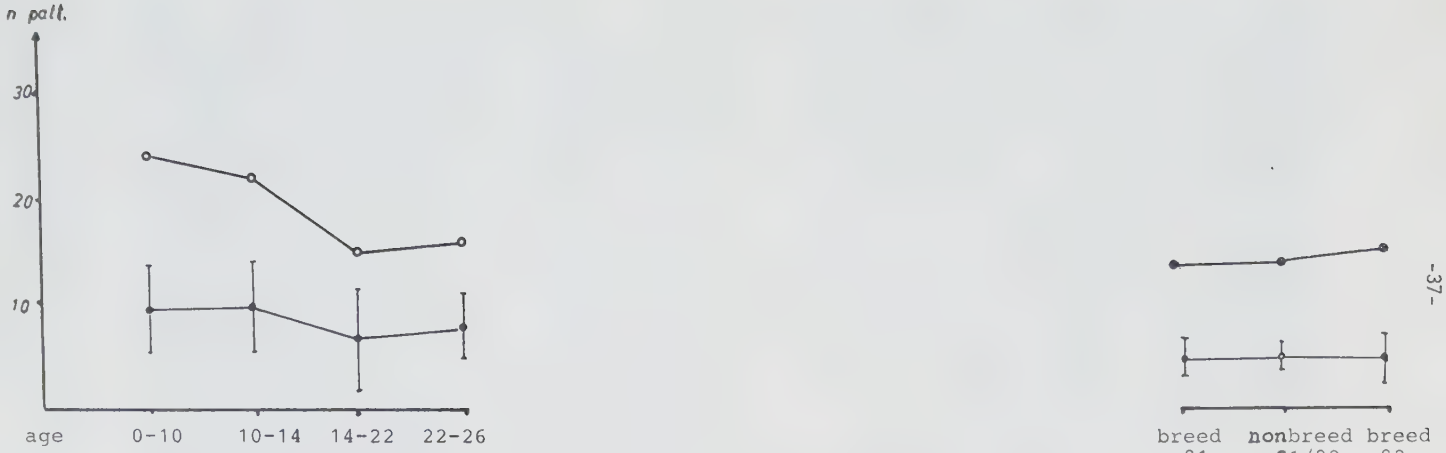


Fig. 11) Absolute and relative variability of social behaviour in females
(○) = abs. var. of foals and yearlings, (●) = abs. var. of adult females
(⧳) = rel. variability of foals and yearlings (⧳) = rel. var. of adult females

The absolute variability in male foals (Figure 10) actually decreased from 30 to 28 in the periods from 0 to 10 months and 14 to 22 months. The variability increased to a high value of 54 during the age period of 34 to 38 months. Thereafter, it decreased to a value of 33 for the period of 58 to 62 months. Generally, the absolute variability of adult bachelors (age 50 to 62 months) was lower than in adult stallions and did not show seasonality as the adult male values did.

The development of the relative variability in bachelors was quite different. It increased from a low value of 12 patterns in foals and yearlings to a high of approximately 30 patterns at age 38 to 46 months. It then decreased slightly to the level of adult males by the period of 58 to 62 months. The relative variability in harme group bachelors, age 46 to 62 months, was significantly higher than in adult males (breeding season 1981, $p \leq .0015$; nonbreeding season 1981, $p \leq .02$, Mann-Whitney U-test). Only in the last bachelor season did male and harem group bachelor values match.

In general, the absolute variability was twice as high as the mean relative variability in both young and adult males. Furthermore, the standard deviations of the relative variability were relatively small.

The relative variability of mothergroup bachelors actually decreased after their first year to a low of 10 different patterns. It increased only after their second and third year of life. It never reached the value for same-aged bachelors in bachelor groups. After sexual maturity, the values of harem group bachelors, which during the third breeding season (age 34 to 38 months) had been the lowest of this age group, increased and reached the adult male levels at 38 to 46 months. However, the harem group bachelors never reached the values of 'true' bachelors of the same age. In general, contact with females in immature males decreased the number of different behavior patterns within a given age period.

The absolute variability in adult females (Figure 11) was 12 patterns on the average; the relative variability was only 4 patterns. This means that an adult female, on the average, showed only four different social behavior patterns over the 1½ year observation period. This was considerably less than what was found for the adult males. In the females, the standard deviation was very small and the absolute variability was about two times as large as the relative variability.

Young females showed a type of development of variability different from young males. The females' absolute variability was highest in foals (25 patterns). It decreased within two years to 15 patterns and then remained on the adult level.

The relative variability of 10 patterns in the foal period (0 to 10 months) remained stable through the first breeding season, but then decreased to the adult female level. The difference between the absolute and relative variability was as large in young females as in adult females and males.

There was no significant difference between male and female foal values for relative variability. Yearling males which leave their mothergroup after the first breeding season showed a significantly higher relative variability ($p \leq .015$, Mann-Whitney U-test) than females of the same age. Mothergroup bachelors did not differ significantly from same-aged females in their relative variability.

Mother-Infant Distance

In order to determine if, and possibly to what extent, a change in the mother-foal relation would contribute to the male and female dispersal on Bird Shoal-Carrot Island, I correlated the number of male and female foals and yearlings which left their mothergroup with the birth of a sibling. The following table presents these data.

Age: 1 year	With Newborn Sibling		No Sibling	
	Male	Female	Male	Female
Left group	9	4	1	0
Stayed	3	0	7	3

($p \leq .01$, Fisher Exact Probability Test)

Age: 2 years	With Newborn Sibling	No Sibling
	Male	Male
Left group	2	5
Stayed	1	1

($p \leq .5$, Fisher Exact Probability Test)

Significantly more male and female yearlings with newborn siblings left their group than males or females without siblings. In two-year-old males, there was no correlation between the dispersal and the birth of siblings. In fact, most of the animals left their group whether or not new siblings were born.

The birth of foals also influenced the relative proximity of yearlings of both sexes to their mothers. The spatial distance between foals and their mother (in relation to the mean spatial distance between members of the nucleus group, see Figure

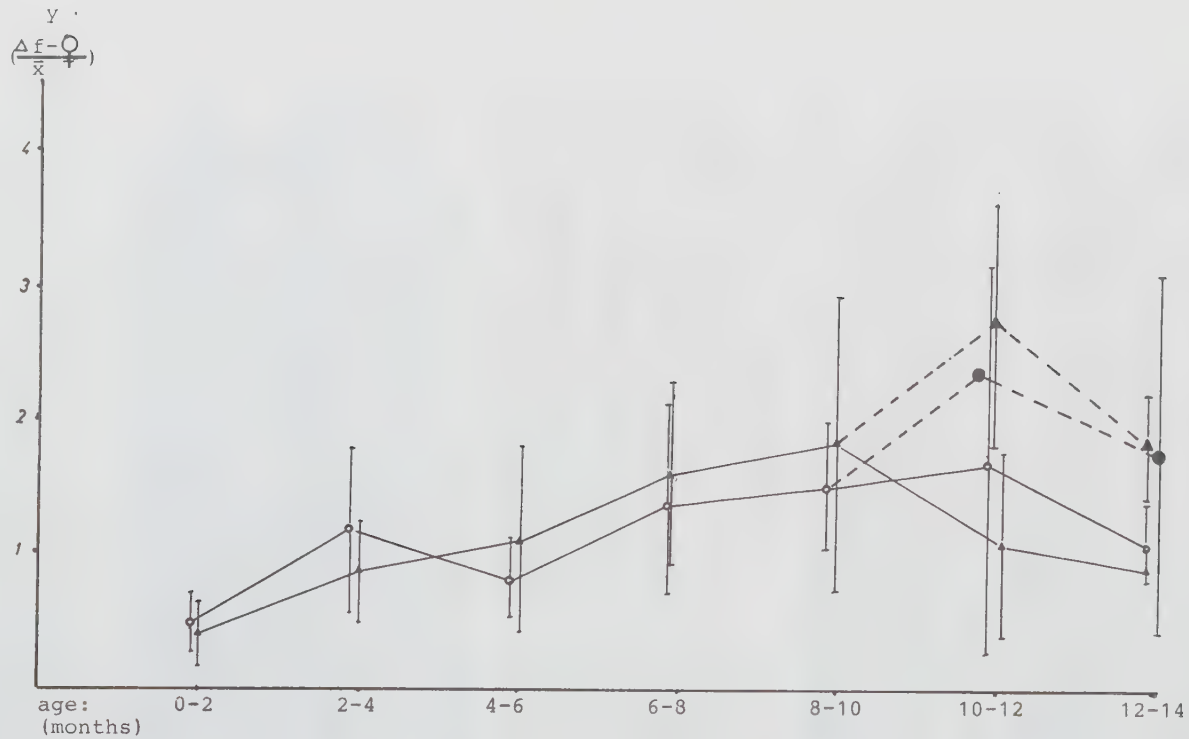


Fig.12) Relative distance of foals to their mother

($\bar{x}$ = mean of av.distances of every adult harem group member to every other harem group member/obs.hour;
rel. distance of foals (Δf-♀) is the abs. av. distance / obs.hr between mother and foal, divided by $\bar{x}$;

y=1 means that the average distance between mother and foal / obs.hr was as large as the av. dist. bewteen every groupmember and every other group member)

12) increased with the increasing age of the foals. After six months of age, foals of both sexes were, on the average, already further away from their mother than the average intragroup distance of the same time. During their first breeding season, both males and females maintained this distance or even decreased the average distance unless a sibling was born. Both male and female yearlings with siblings were, on the average, twice as far away from their mother than 'non-sibling' yearlings. Their distance to the nucleus group was similar to the distance kept by subdominant males to a harem group. They were not driven by the stallion anymore.

First Occurrence and Horse Frequency of Social Behavior Patterns

The individual frequency of occurrence of each of the 59 observed patterns varied extensively between horses, age periods, and contexts. This was due to the overall low rate of social activity in the horses and to the individual differences in the choice of patterns. In order to determine the actual structure of development within one behavioral category, it seemed appropriate to simply measure the frequency for every pattern in terms of the number of horses that displayed it (that is, the horse frequency).

Playing Behavior (Figure 13a)

There were seven different playing behavior patterns. In adult males, the horse frequency of play was strongly seasonal. During the breeding season, only low-key playing activity was observed (Patterns 39 and 9a). In the nonbreeding season, all patterns occurred. The horse frequency of play in adult males was very low. At any given season, only 10 to 20 percent of the horses showed playing behavior patterns.

The majority of the male foals and yearlings used the low-key playing patterns (Patterns 39, 6a, and 9a). Only once did a yearling show a playing pattern with agonistic character (Pattern 10a, front hoof beating). The high-intensity playing patterns (Patterns 11a and 12a) were not observed to occur before the second breeding season, and then, only in a very few males. The horse frequency of low-key patterns peaked between the age of 22 to 38 months. The high-intensity patterns peaked between the age of 34 and 50 months, indicating a correlation between first occurrence, peak horse frequency, and intensity of playing behavior patterns.

Fewer adult bachelors showed less playing patterns that did adult stallions. In fact, most of the patterns were not observed at all in bachelors aged 50 to 62 months.

Playing behavior was not observed at all in adult females except for two instances in which an adult female initiated the play (Figure 14a). In female foals age 0 to 10 months, the first occurrence and horse frequency distribution of playing patterns was similar to the male foal distribution. Initiating play and chase occurred in almost all female foals, but snap-wrestle and bite-play occurred in less females than in males. With increasing age, both the number and frequency of playing patterns in females decreased. This is contrary to the development of play in male yearlings.

Grooming (Figure 13a)

All three types of grooming were used by adult males, but only by 20 to 30 percent of them during the breeding seasons. Allogrooming was observed in all male foals, however, its horse frequency decreased with age. Mutual grooming occurred in foals, but was not observed in all males until the age of 14 to 22 months. Thereafter, mutual grooming decreased to the adult male horse frequencies.

As in adult males, only 20 to 30 percent of the adult females showed passive mutual grooming or allogrooming during any season (Figure 14a). Contrary to the adult male pattern, the adult females did groom during the nonbreeding season. In young females (0 to 10 months), all three grooming patterns were observed. However, one major difference was that relatively more young females than young males used the passive grooming patterns rather than the active, initiating pattern. The young female horse frequencies of grooming decreased with age.

Agonistic Behavior (Figure 13b)

I observed 11 different agonistic behavior patterns with varying intensity in the males on Bird Shoal-Carrot Island. Adult males used all forms of agonistic behavior. The horse frequency decreased with increasing intensity.

Simple low-key (no body contact), defensive patterns were found in some foals (Patterns 7, 8, and 3). The horse frequency of these patterns increased with age. The other agonistic behavior patterns appeared successively between the first and third breeding seasons, usually in very few horses at the beginning. Again, just as in playing behavior, the intensity and pattern complexity correlated with the sequence of first occurrence and peak horse frequency. That is, simple, low-key patterns peaked earlier than more complex patterns. All adult bachelors, age 50 to 58 months, used almost all agonistic behavior patterns. Thus, the horse frequency, especially of high-intensity agonistic patterns, was highest in bachelors building up their own harem group.

Except for the ear position (during play, the ears are up or half back; during agonistic behavior, the ears are flat back and vocalization occurs), the agonistic behavior patterns 9, 10, 11, and 12 are identical in stereotypes to the playing behavior patterns 9a, 10a, 11a, and 12a. The time of first occurrence of these agonistic patterns was preceded by the first occurrence of the equivalent playing patterns by one to two seasons. The peak horse frequency of agonistic behavior patterns was preceded by the peak horse frequency of the equivalent playing patterns by three seasons. The horse frequencies of agonistic pattern number 12 and playing pattern number 12a had a seasonally-alternating character. In the breeding season, the horse frequency of agonistic 12 was high and that of play 12a was low. In the nonbreeding season, the frequency of agonistic 12 was low, but that of playing pattern 12a was high.

Although agonistic behavior comprised a major part of the 'social' activity of female horses (Figure 14b), only six of the 11 different agonistic patterns occurred in adult females. Out of these six patterns, four patterns (threat, head beating, chase and bite) were observed in only one or two females. Two patterns (snap and hindhoof kick with vocalization) with defensive, low-key character were used by almost all females in the nonbreeding season and by all females in the breeding season. This distribution is almost identical to the adult male horse frequency distribution for these two patterns.

Female foals, as well as male foals, used these two patterns, together with threat and front hoof beating with vocalization. The horse frequency of the defensive hindhoof kick was higher in female foals than in male foals (60 percent). During the first breeding season, the horse frequencies of all patterns increased, and head beating was observed for the first time in females. At the age of two, females had developed a horse frequency distribution of agonistic behavior patterns almost identical to the adult female distribution.

Submissive Behavior (Figure 13c)

In males, the occurrence of two out of four of the submissive behavior patterns had age-dependent characteristics. Teeth blecking and teeth clapping were observed to occur only in young males, with the highest horse frequency at the age of 22 to 26 months. Adult bachelors and adult males never used teeth blecking and teeth clapping, however, adult females did. Run-away and walk-away occurred in all age groups of males, but most frequently at 34-50 months of age, right after sexual maturity. In sexually mature males, the less intensive, submissive pattern (walk-away) was used by more males in the same age group than run-away. Relatively fewer adult females than adult males showed submissive behavior patterns. Other than

in male foals, teeth clapping was the only pattern observed in almost all female foals. The highest horse frequency of all submissive behavior patterns was found in females in their first breeding season. After this time, submissive behavior declined steadily; however, the male frequencies for submissive behavior patterns increased for the same age groups.

Driving (Figure 13d)

The two forms of driving appeared together in males which had just become sexually mature (age 34 to 38 months). The horse frequency of driving increased steadily and reached 100 percent in the age group 50 to 58 months. Between 80 and 100 percent of the adult males showed driving, independent of the season. Stretch and chase were observed to occur very infrequently in very few horses.

Sexual Behavior (Figure 13e)

Three of the five behavior patterns with sexual character appeared for the first time in male foals: naso-nasal contact with females, sniff genitals of females, and mounting females. Courting females was observed first in males being 10 to 14 months old. Until sexual maturity, the horse frequency of all of the sexual patterns remained very low and some of the patterns were not observed at all in certain age groups. With sexual maturity, the horse frequencies increased and at age 38 to 46 months, the category was completed with the first occurrence of copulation. The horse frequency of all sexual behavior patterns was above 50 percent (courting 100 percent) in adult bachelors trying to build up a harem group (age 58 to 62 months). Mounting and copulation were not observed in the nonbreeding season in adult group stallions, but did occur in sexually mature bachelors.

The sexual behavior patterns discussed above could not be observed in females. Only presenting (Pattern 31) was identified as an observable behavior pattern. Females presented only when they were in heat.

Defecation Marking (Figure 13f)

All adult stallions showed complete marking of old defecation piles (Pattern 28); while many of the adult stallions, but not all, showed complete marking of fresh piles (Pattern 24) and the simple, sniff-pile pattern. In adult stallions, all other forms of defecation marking were observed very infrequently.

The simplest marking-related pattern (sniff pile) occurred in almost all foals, independent of the type of stimulus (fresh or old pile). The horse frequency of this pattern remained constantly high throughout life. Complete marking behavior (Patterns 24 and 28) occurred first in bachelors aged 26 to 34 months. The horse frequency for complete marking behavior increased steadily with age and was represented in all bachelors at and after the age of 46 to 50 months. The horse frequency for complete marking behavior was seasonally independent in both adult bachelors and adult stallions.

The three forms of incomplete marking behavior (Patterns 21b and 25b, 22 and 26, and 23 and 27) preceded the complete marking behaviors both in their first appearance (foal and yearling age periods) and their peak frequency (34 to 46 months). Two patterns (sniff pile, defecate and sniff pile, marking position) showed almost no difference in their horse frequencies and distributions over age. At no age did more than 30 percent of the bachelors use either pattern, and after 38 to 46 months, these patterns were not observed at all. The combination of these two patterns (Patterns 23 and 27) occurred first at 22 to 26 months, with the horse frequency increasing until age 38 to 46 months. Thereafter, these patterns decreased in frequency, corresponding with the increase in complete marking. In young males, the fresh pile marking patterns had a higher horse frequency and occurred earlier (in case 21b and 25b) than the old pile marking patterns.

None of the maturing bachelors were observed to suddenly use complete marking. All of them, except for possibly one, used some form of 'precursor' before showing complete marking.

Adult females did not use the actual defecation marking pattern (Figure 14f). Some females sniffed piles on very rare occasions. Generally, the same was true for female foals. The only commonly represented pattern for the females was sniff fresh pile. Sniff old pile did not occur at all. The horse frequency for the defecation marking pattern decreased with age. In two instances, I observed a female sniffing a pile and defecating moments later. These two instances could represent the pattern sniff pile, defecate.

Urine Marking (Figure 13g)

Male horses marked both feces and urine with their own urine. Both forms of urine marking were observed to occur in some male foals. Flehmen and the olfactory investigation of urine and feces with flehmen also occurred in some male foals. The complete form of urine marking, with flehmen and the 180^{o} turn, appeared later in life, specifically at the time of sexual maturity.

In two-year-old bachelors, only sniff urine, flehmen, and sniff feces, flehmen were observed. Relatively few of these bachelors urine marked feces. Although all forms of urine marking occurred in three-year-old bachelors, their horse frequencies were very low except for the sniff feces, flehmen and sniff urine, flehmen patterns. The horse frequency distribution typical for adult males developed rather suddenly at the age of 50 to 62 months. All males showed urine marking on feces and most of them urine marked on urine.

The development of urine marking in males reveals that almost all patterns, including the complete forms of urine marking, were present in foals; however, bachelors used only investigatory patterns with flehmen. The combination of flehmen and complete urine marking occurred later, usually with sexual maturity. Sniff urine, the supposed equivalent to sniff feces, was almost never observed. Thus, almost every investigation of a urine spot led to flehmen or marking activity.

Very few adult females (Figure 14g) showed urine marking during one of the three seasons (sniff urine, marking position, urinate). No other form of urine marking nor flehmen was observed in adult females. Unlike male foals, the female foals urine marked on feces. Female yearlings abandoned urine marking of feces and flehmen (while male yearlings developed these patterns) in favor of urine marking of urine, which almost all female yearlings practiced.

It has to be noted that the young females' urine marking of urine had exactly the same appearance as the 'sexual presenting'. It is therefore possible that this urine marking of urine had a sexual characteristic rather than a marking characteristic.

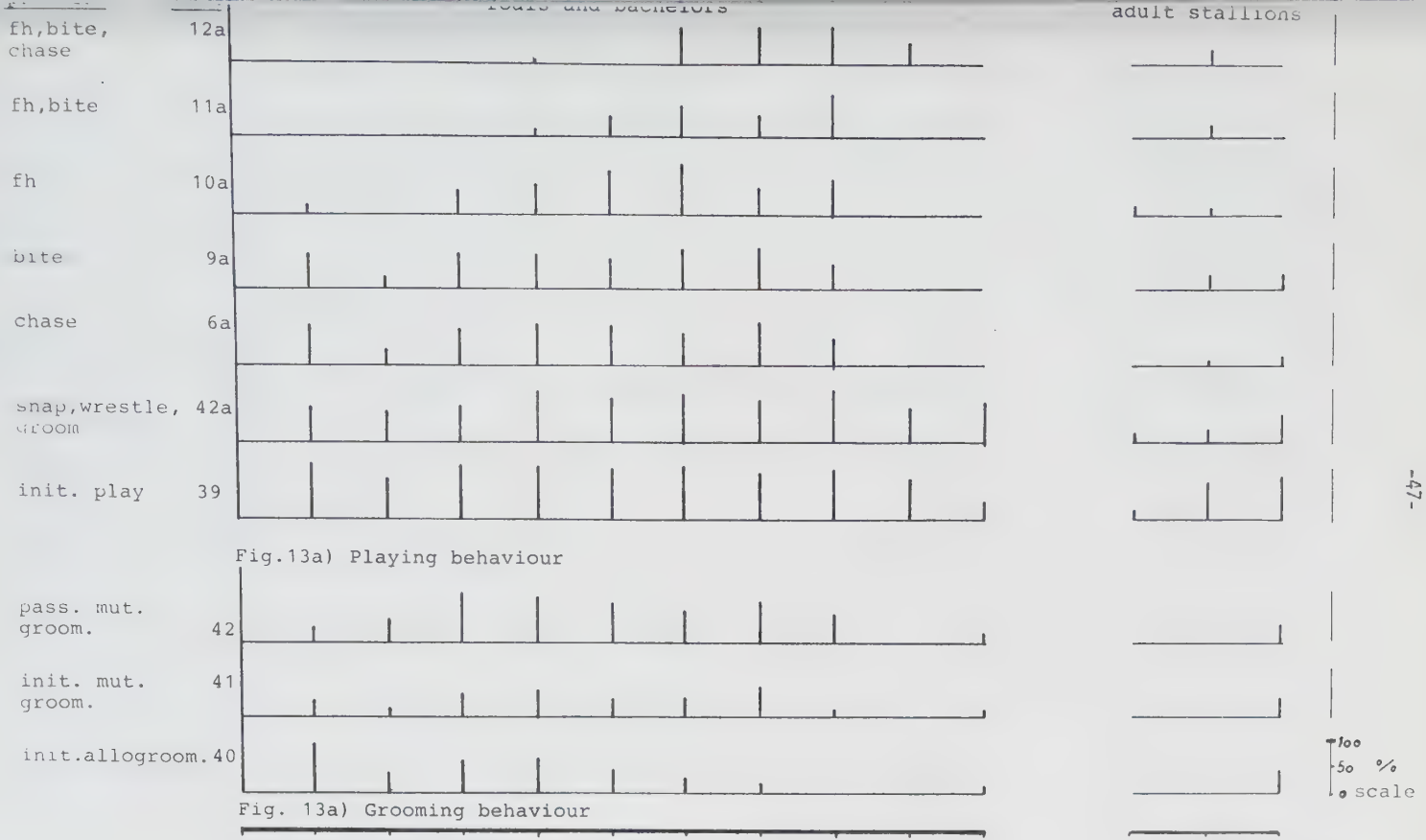


Fig.13a) Playing behaviour

Fig. 13a) Grooming behaviour

Fig.13) First occurence and horse frequency of behaviour patterns in males;
(| = the number of horses in which this patterns was observed to occur, in relation to all horses of this age period (%); 100 % = 1 cm (see scale)

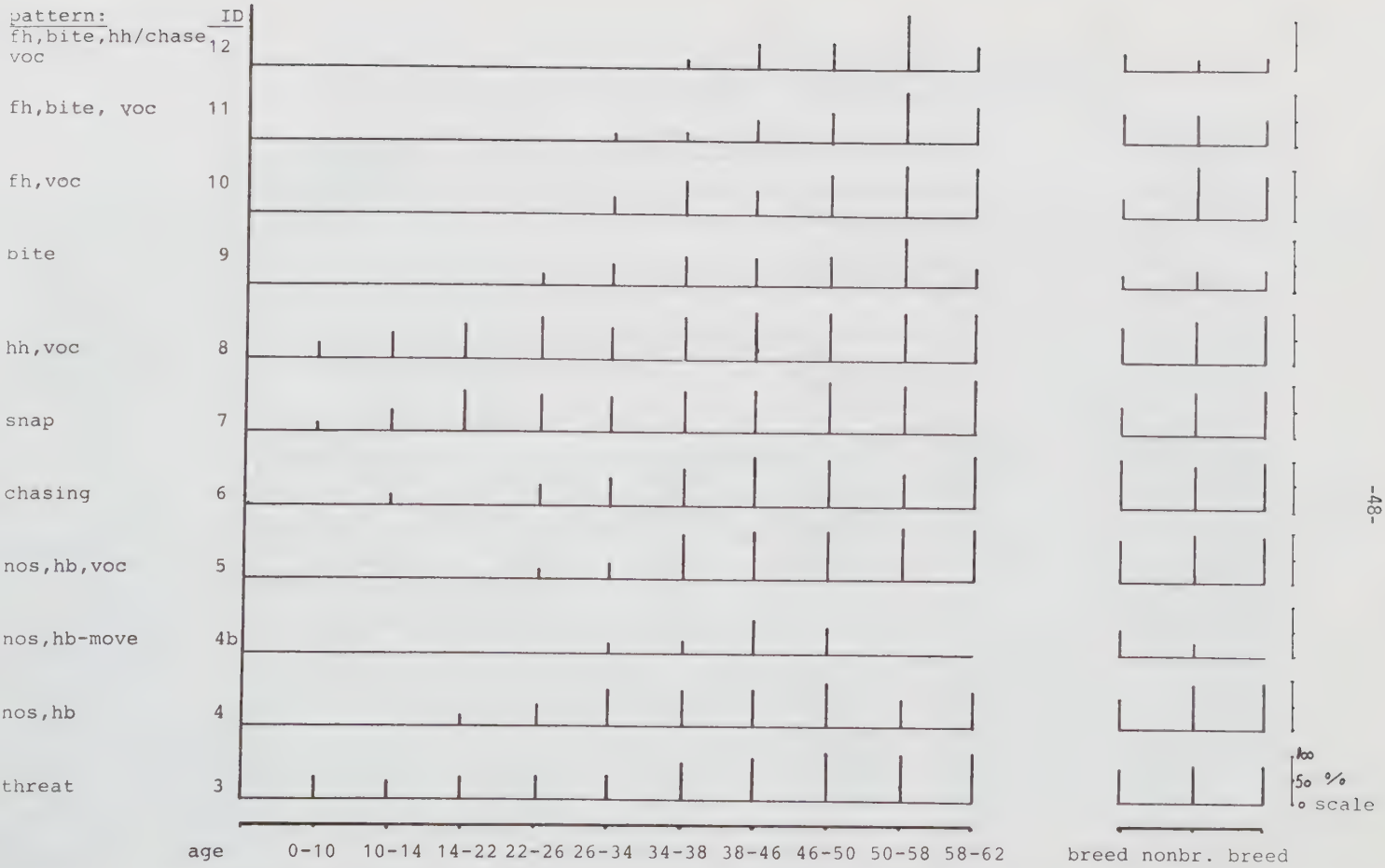


Fig.13b) First occurence and horse frequency of beavior patterns in males; (legend see 13a) agonistic behaviour

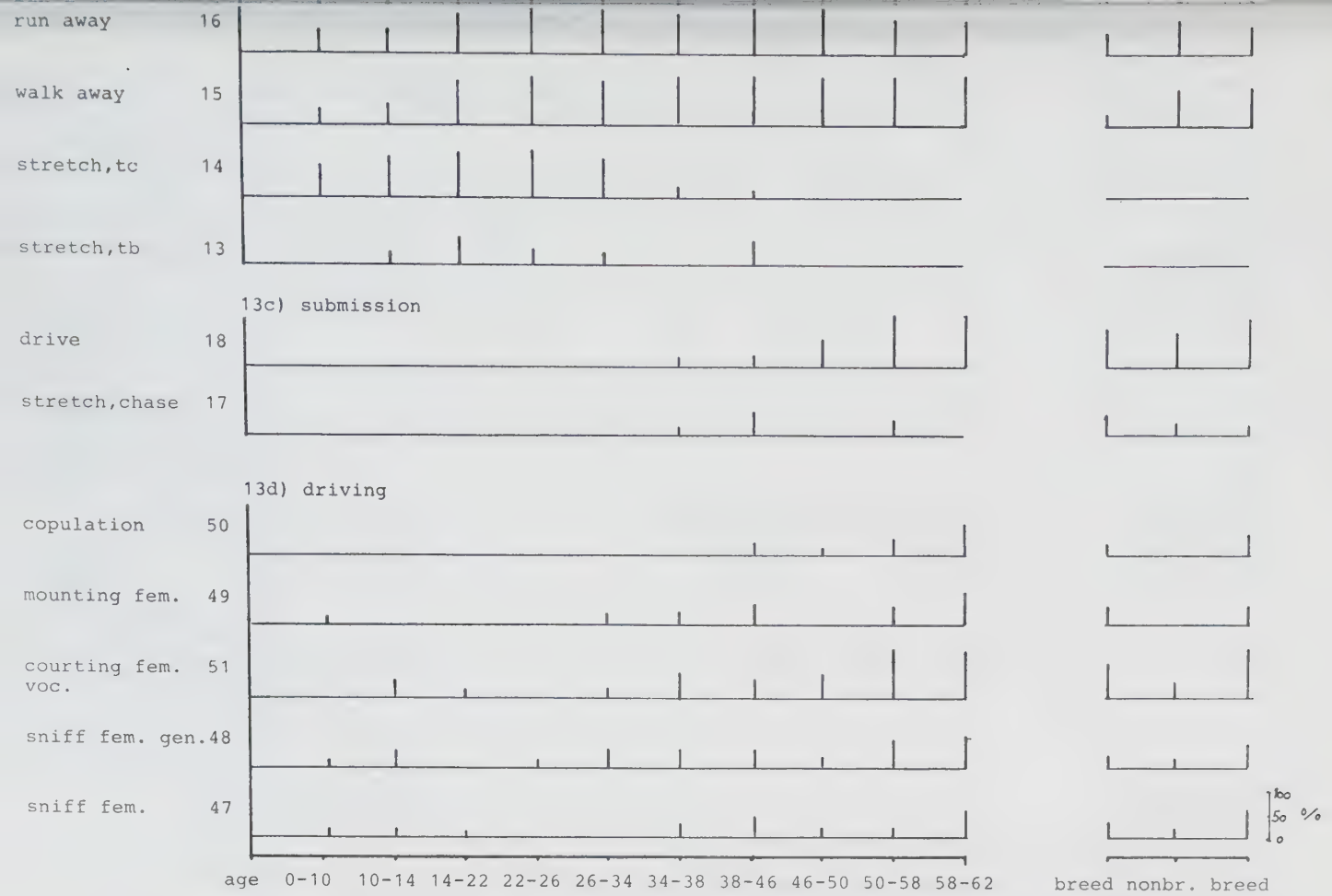


Fig. 13) First occurence and horse frequency of behaviour patterns in males; (legend see 13a)
13e) sexual behaviour

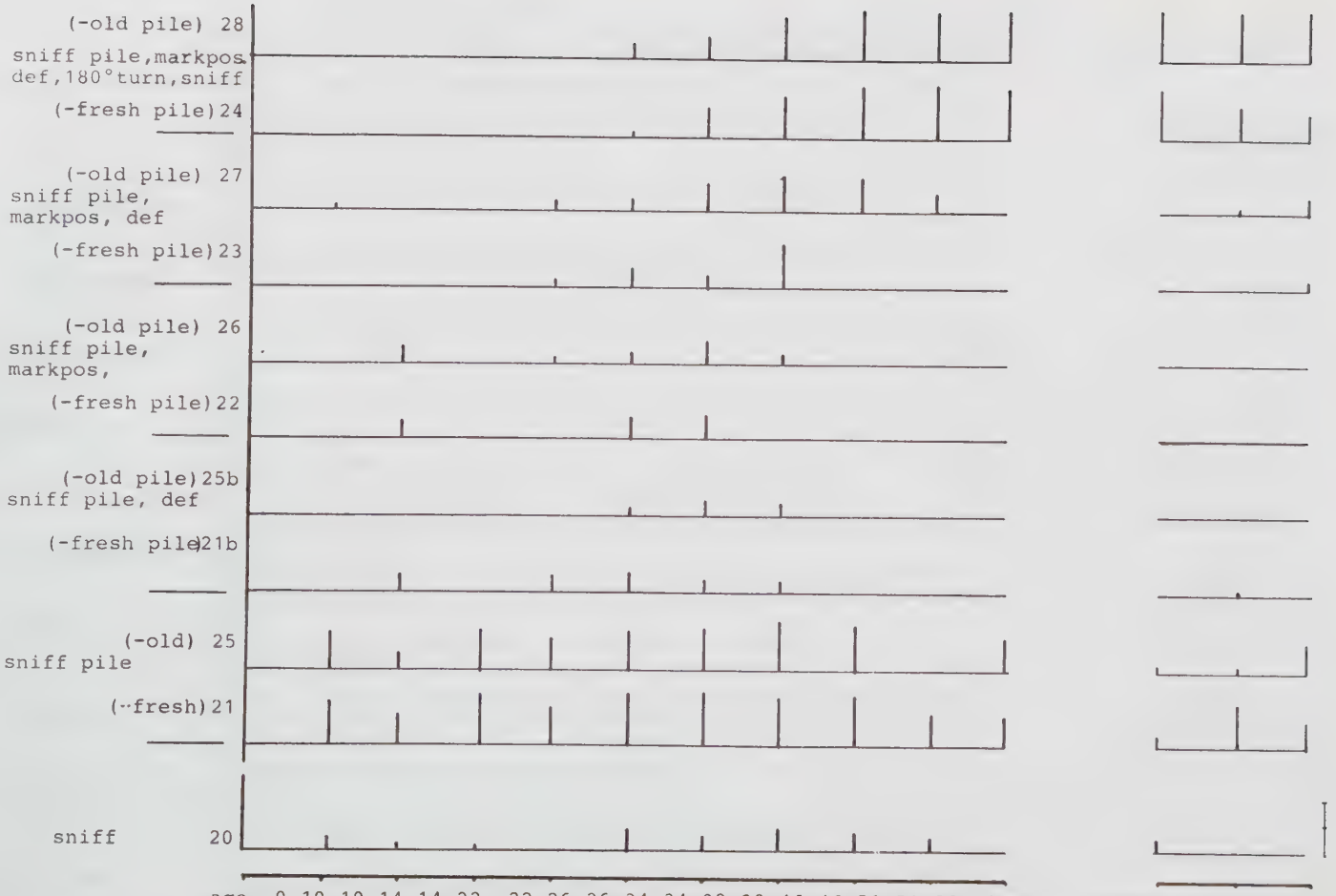


Fig.13f) First occurence and horse frequency of behaviour patterns in males defecation marking

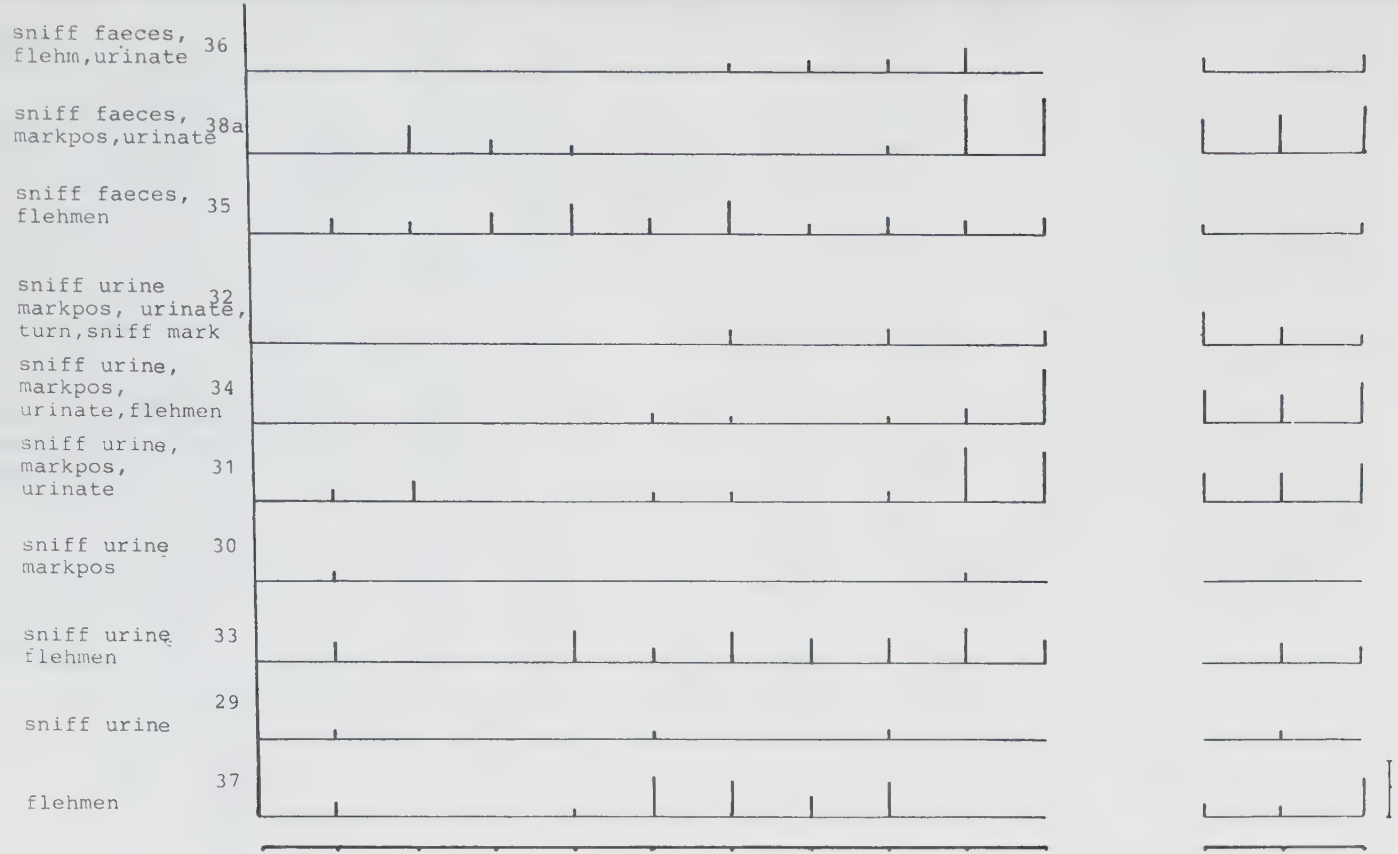


Fig.13g) First occurence and forse frequency of behaviour patterns in males urine marking

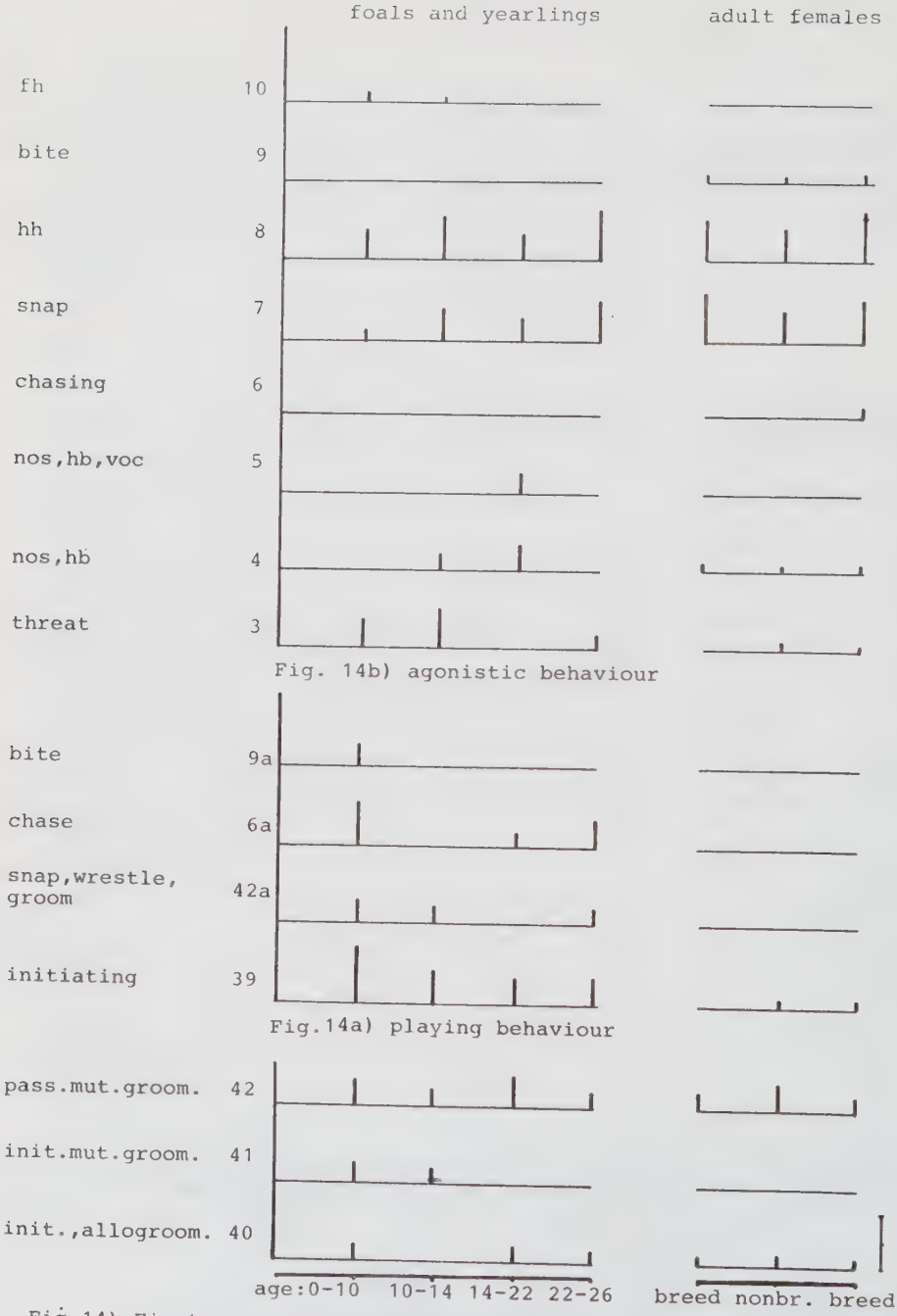


Fig. 14b) agonistic behaviour

Fig.14a) playing behaviour

Fig.14) First occurence and horse frequency of behaviour patterns in females; (legend see Fig.13)

Fig.14a) grooming behaviour

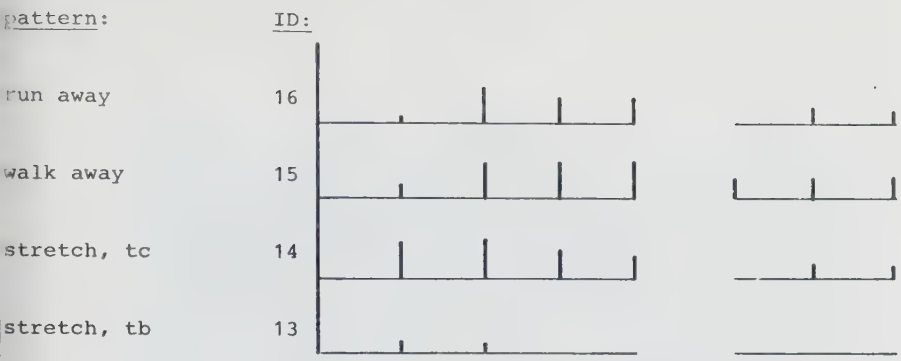


Fig. 14c) submissive behaviour

Fig.14g) urine marking

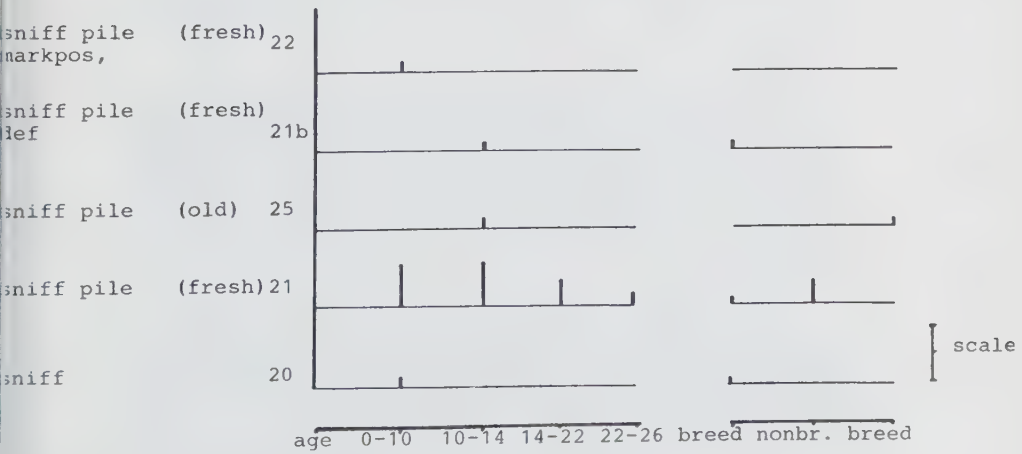


Fig.14) First occurence and horse frequency of behaviour patterns in females

Fig.14f) def.marking

SUMMARY

The social behavior and its ontogenetic development was observed in all individuals of a feral horse population on an island off the North Carolina coast from 1980 to 1982. The social organization and population dynamics of the studied population resembled those of other truly feral horse populations. The horses lived in stable harem groups comprised of one stallion, several (two to four) mares with their immature offspring, and sometimes a subdominant sexually mature male. The mares were controlled and bred only by the stallion. Young males lived singly or in loose bachelor associations (bachelor groups) until they built up their own harem group, generally at the age of 4 or 5 years. Young females left their maternal group during their first estrus and joined another harem group. They became reproductive between the age of 2 to 3 years.

The social activity of the horses was defined and measured as the frequency of occurrence of the behavior patterns of the following social behavior categories: agonistic behavior, submissive behavior, playing behavior, greeting, grooming, sexual behavior, driving, defecation marking, and urine marking. The frequencies of these categories were compared over age, season (breeding versus nonbreeding), social context (female present versus no female present), and sex. A total of 59 different behavior patterns were observed to occur in the males. Thirty-three of these patterns were observed in the females.

The total frequency of social behavior varied seasonally between 0.3 and 0.5 events per observation hour per horse in adult females and 2 to 3 events per hour per horse in adult males. Female foals were socially less active than male foals, and male foals showed less social activity than immature or adult males.

In adult males and females, agonistic behavior was observed to occur most often and comprised the major portion of their social behavior (between 40 and 80 percent). In males, defecation marking and driving were the next most frequent behavior categories. Non-competitive social behaviors (such as play and grooming) were observed very infrequently in the males. Adult females did not display driving, urine marking, defecation marking, or play, and very infrequently showed grooming or greeting behaviors.

The socialization period of immature males lasted from birth until the age of five years when they became reproductive. The socialization process was categorized into three phases with differing sets of frequency distributions of social behavior. These three phases are:

(1) In foals and yearlings (age 0 to 22 months), the frequency of occurrence of social behavior was fairly evenly distributed over the non-competitive categories of grooming, play, greeting, and submission. Role-specific behavior categories either did not occur at all (driving) or appeared only sporadically in incomplete form (for example, defecation marking or urine marking). Simple behavior patterns were used more often than complex ones. The average individual behavioral variability (number of different patterns used by an animal) was the lowest of all age groups. Males which left their maternal group (50 percent) spent significantly more of their activity on agonistic and submissive behaviors than did males remaining with their mother. Departure of male and female yearlings from their maternal group generally coincided with the birth of a sibling.

(2) Between the age of 22 and 38 months, all bachelors had left their maternal group and joined bachelor groups. Males remaining in their maternal group until the age of three years spent significantly more of their social activity on agonistic and submissive behavior than bachelors did. On the average, these mothergroup bachelors used only half the number of different behavior patterns than 'true' bachelors did. In bachelors, playing was by far the most frequently observed social behavior. Almost all behavior patterns of the role-specific categories had occurred during this age period, and their frequency of occurrence slowly increased with age. The frequency of grooming and submission, however, decreased. The behavioral 'precursors' of defecation marking and urine marking (incomplete forms of complex behavior patterns) were observed to occur more frequently. Agonistic play patterns were increasingly substituted by their agonistic counterparts. The individual behavioral variability reached its highest value of any age period.

(3) Between the age of 38 to 62 months, sexual maturity in bachelors was reached. At this time, they increasingly built up harem groups. At the age of 62 months, all bachelors were stallions or subdominant stallions in a group. During this phase, the whole set of behavior categories shifted both in qualitative structure (first occurrence, types and frequencies of patterns) and quantitative distribution (frequency of occurrence of categories) until the adult male pattern was attained. Generally, the frequency of play and grooming behavior decreased while the frequency of agonistic behaviors, driving, and marking increased. The social activity of these bachelors was strongly social-context dependent. As bachelors, they played and groomed more frequently, had less agonistic and more submissive encounters than they did as harem group 'owners'. As bachelors, they showed no sexual activity, driving, or urine marking. The time span of successfully keeping one or more females increased with age. Young, inexperienced bachelors primarily used an immature or old, unreproductive female to form their own harem. With increasing age, they abandoned these females in favor of adult, reproductive females.

The female development of social behavior differed from the male type of development. Female foals showed no qualitative and little quantitative differences in their social activity when compared with male foals. Most of the females left their maternal group when they had their first estrus. Thereafter, they reduced both the number and frequency of social behavior patterns, until the adult female frequency and type of social behavior was attained. The immature and adult female social activity was so low (0.4 to 0.8 total social events per observation hour per horse) that the author's method of investigation was not suitable for quantitative analysis of the females.

DISCUSSION

According to the data obtained in this study, the development of social behavior in maturing horses differed with respect to age, sex, and within the males, to the presence or absence of adult females (social environment). In general, female foals were less active than male foals as measured by their overall social activity. Female foals also tended to nurse and rest more often than male foals. However, there was no significant difference between male and female foals in the absolute and relative frequency distribution, the first occurrence, and the number and type of patterns observed for any behavior category (except urine marking).

Foals of both sexes used the simple, low-intensity non-agonistic social behavior patterns. The two different agonistic patterns observed to occur in foals were normally used by adult females to control intragroup hierarchies and protect foals. Male foals showed more different types of urine marking and more often than did female foals.

Only few quantitative data are available in the literature on the occurrence, frequency, and distribution of social behavior in feral foals. The first occurrence, sequence, and frequency of behavior patterns in New Forest foals (Tyler 1972) differed from the occurrence in Bird Shoal-Carrot Island foals. New Forest foals seemed to play and groom much more among each other and with subadult and adult animals. Colt foals played rougher than fillie foals, using patterns observed in adult males during serious fights. Fillie play mostly consisted of grooming and simple agonistic patterns. New Forest foals nursed and rested more often than Bird Shoal-Carrot Island foals, as illustrated in the table below.

AGE	NEW FOREST	BIRD SHOAL-CARROT ISLAND (See Figure 5b)
0 - 8 weeks	2.5-3 bouts/hour	1.4 bouts/hour
8 - 16 weeks	1.7 bouts/hour	0.8 bouts/hour
16- 24 weeks	1.0 bouts/hour	0.5 bouts/hour
0 - 8 weeks	50 - 60 percent*	45 percent*
8 - 16 weeks	50 percent	25 percent
16- 24 weeks	40 percent	25 percent

(* Percent of total observation time)

Unfortunately, no standard deviations for nursing frequencies are available on the New Forest foals. This fact did not enable discussion of their population specific variability.

Wells and Goldschmidt-Rothschild (1979) report a median frequency of 4.64 events per hour for three different agonistic patterns, friendly contact, and allogrooming in Camargue foals. They derived their data from seven foals of both sexes between May and September. Bird Shoal-Carrot Island foals, on the other hand, showed a total mean of 1 to 2 events per hour, including every social activity.

Many studies have been conducted on ontogenetic aspects of domestic foals (Grzimek 1949a, Waring 1970b, 1972, 1983, Williams 1974, Fagen and George 1977, Boy and Duncan 1979, Fraser 1980, Fagen 1981). The results of a recent project indicate that significant differences exist between foals of different ages and sexes in the frequencies of occurrence of certain play behavior patterns (Klopfer-Honoré 1983). Unfortunately, no data on the absolute frequencies are available yet.

Obviously, foals of other feral horse populations seem to have been much more active in social contact and play than the Bird Shoal-Carrot Island foals. Domestic foals in a similar climate and seasonal condition even showed significant quantitative differences between sexes (Klopfer-Honoré 1983).

I assume that the lower overall frequency of social activity, resting, nursing, and possibly the small sex differences in foals on Bird Shoal-Carrot Island were the result of the environment and social system which consisted of small harem groups with usually not more than two foals, two mares and few yearlings, highly competitive group stallions, and subdominant stallions. Furthermore, the extremely harsh environment may not have provided enough time or potential partners for an exchange of social bouts equivalent in occurrence, frequency, and distribution to Camargue foals, New Forest foals, or truly domestic foals. Wells and Goldschmidt-Rothschild (1979) derived their results from an unusually high number of young individuals living together in a single herd in the Camargue. Tyler's description of the New Forest mares (and their offspring) indicates that they established larger groups when grazing together. If and to what extent these differences (for example, the 'lack' of social contacts) actually influences the maturation process and contributes to the adult animals' performance is not yet known. Further studies on this population and on other feral Equid populations are necessary to quantitatively complete the few preliminary data on foal development.

At the age of one year, 50 percent of the male and female foals on Bird Shoal-Carrot Island left their group. The time of departure of young females usually coincided exactly with their first estrus (two females actually gave birth a year later). Furthermore, a strong, significant correlation between the birth of a sibling and the male and female dispersal was observed in year-old foals. In both sexes, the mother-foal distance differed between yearlings with siblings and yearlings without siblings.

Tyler (1972) reports that the majority of the New Forest fillies did not leave their maternal group. Among those who did leave, most did so after the third year of life. No data on the New Forest male dispersal is available due to the artificial sex ratio in the population (Tyler 1972). In all other feral horse populations and polygynous zebra species, both male and female dispersal is observed with differing frequencies in the various age classes (Feist 1971, Klingel 1974, Keiper 1976a, and Goldschmidt-Rothschild and Tschanz 1978). Feist reports that all yearlings stayed with their group, but 29.9 percent of all immature females (no ages were given) changed bands during the breeding season. Keiper (1980) observed that most immature animals on Asseteague Island (USA) had left their group before they were two years of age.

The mechanisms and functions of both male and female dispersal in polygynous Equid species are not yet known. Furthermore, they may be different for both sexes. The data from Bird Shoal-Carrot Island reveal that sexual maturation in females may have elicited departure from the mothergroup. This seems to confirm observations that horse harem stallions normally do not mate with their young, in-group offspring (Waring 1983). Collery (1969) reports that normally horse stallions do not try to keep yearling females in their group. Jaworowska (1980) even observed that stallions actively chased their female offspring away. Franklin (1974) observed this same dispersal in the territorial vicuñas. Klingel (1972) reports that in plains zebras, yearling estrous females were actively stolen from their mothergroups by other males against the apparent will of the stallion. (It is not clear whether the stallions were the fathers also.)

The social bond between mother and infant in horses may partly be expressed by the distance between them. The disruption of this bond by the birth of a sibling may be a second, external cause of juvenile dispersal at the age of one year. In foals on Bird Shoal-Carrot Island, the average distance to the group increased with age. The birth of a sibling apparently produced the actual spatial separation which normally would have occurred anyway a year or two later. The separation would have coincided with a drastic increase of agonistic and summissive behaviors in the young males. This was not observed in same-aged bachelors already living in bachelor groups.

After the age of one year, females had joined other harem groups where they assumed reproductive positions comparable to the adult mare position. By this time, they had shown 90 percent of the female social behavior patterns. In addition, they began to modify their set of social behavior patterns in such a way that they reduced their flexibility (the absolute number of different patterns) and changed the relative frequency distribution of the various categories towards the adult female set. They abandoned marking and play, and increasingly they showed agonistic and submissive behavior.

Wells and Goldschmidt-Rothschild (1979) observed that Camargue mares showed very little overt non-aggressive behavior. Some mares were never observed to groom, and some did not play at all. Male yearlings played significantly more than female yearlings. Goldschmidt-Rothschild and Tschanz (1978) investigated a group of mixed-sex young Camargue horses and found that young mares did not participate in play-fights. They were more intolerant towards strange females than were young males towards strange young males. Both Tyler (1972) and Feist (1971) did not specifically investigate the behavior of young females. Tyler does mention that young mares were more tolerant of foals playing with them than older mares were in the same situation. Tyler even observed adult mares showing complete marking behavior.

Thus it generally appears that in other Equid populations, there are both quantitative and qualitative differences in the social behavior between yearling males and females, even in a similar social environment (for example, Camargue mixed-sex groups). Due to the lack of information, any further discussion of the development of social behavior in adolescent females would be purely speculative at this point.

In my opinion, the number of females and the number of observation hours in this study were extremely low, considering the 'cryptic' behavior of the females. This behavior was expressed by the frequencies of occurrence of most behavior patterns, or even categories, and the extreme individual variability in behavior. I believe that the author's methods were not suited for quantitative investigation of the development of females.

The development of males after their first year differed significantly from female development. After an initial 'stagnation' at the age of 1½ years (a period of almost no change in any of the investigated parameters), the males rapidly increased the number of different patterns and the frequency of the various categories which they used. At the time of sexual maturity (2 to 3 years), a male had shown almost all adult male-specific patterns, except for driving and copulation. Males were also able to use all agonistic and marking patterns in the right competitive contexts, but rarely did so. Behavioral 'precursors' were observed to occur in the marking and play categories. These precursors were age-specific and were not observed in adult males.

In fact, while the qualitative development of social behavior proceded with sexual maturation, the distribution of the relative frequency differed from both the foal type and the adult male type of distribution. The bachelors spent the majority of their social interactions on playing behavior (40 to 60 percent), practicing both low-intensity and high-intensity patterns.

The high-intensity playing patterns were identical to the high-intensity agonistic patterns, except for the non-agonistic ear position and the absence of vocalization. Bachelors remaining in their maternal group after their first year of life showed a different type of frequency distribution. Their absolute frequencies of social behavior categories differed significantly from the distributions of same-aged females in the same way that the frequencies of the 'true' bachelors did. On the other hand, the mothergroup bachelors used fewer different patterns and spent significantly more time on agonistic and submissive behaviors than same-aged 'true' bachelors.

The transition from the foal state to the state of sexually immature bachelor was irreversible. Bachelors leaving their mothers' group never returned to it. A very early transfer from the foal to the bachelor state (for example, 10 to 14 months) was accompanied by a high occurrence and relative distribution of agonistic and submissive encounters which they exchanged primarily with mature bachelors and other group stallions. A very late transfer was preceded by a very high absolute and relative frequency of agonistic behavior (26 to 34 months) and submissive behavior (22 to 26 months) which were both directed against the group stallion.

In other feral Equids, such as the mountain zebra (Joubert 1972), feral asses (Woodward 1979), domestic horses (Fagen 1981, Waring 1983), and semi-feral populations (Wells and Goldschmidt-Rothschild 1979, Tyler 1972), playing behavior seemed to be the main social activity also. Unlike in the bachelors on Bird Shoal-Carrot Island, the play in foals and yearlings of the Camargue and New Forest populations already contained fighting elements normally found only in adult males. This seems quite surprising and I cannot readily explain this difference. Probably the presence of a dominant stallion in Bird Shoal-Carrot Island harem groups surpressed every play behavior with competitive elements. Feist (1971) observed a similar control of social play in immature group members by the stallion. This may also explain the differences between bachelors and same-aged mothergroup bachelors. In the latter, the absence of same-aged peers and the constantly 'serious' environment forcefully reduced the individual flexibility (number of patterns), choice, and proper application of adult male-specific behavior patterns.

On the other hand, most of the new behavior patterns occurred first in males in contact with females. I therefore assume that many stimuli for the first appearance of patterns may lie in the social environment of a harem group. The actual practice and application in the proper context may have been possible, though only in a social environment free of serious competition, such as the bachelor group.

The actual competitive use of the newly-achieved patterns was observed in the third phase of socialization. This phase lasted from sexual maturity until the male reproductive state which is characterized by the permanent association with adult females. In this period, the position of bachelors alternated between the bachelor status and the harem-group bachelor status. Harem group bachelors tried to build up their own harem group. This social position became the dominant position with increasing age. These adult bachelors abandoned adolescent-specific patterns. Their behavioral flexibility was the highest of all males. They even used more different patterns than adult stallions did. Their absolute and relative frequency distribution changed towards the adult male-specific distribution pattern. These sexually mature bachelors were never observed to 'steal' mares or even try to do so. Instead, they joined female yearlings when they left their group or stayed with old, unreproductive mares. These 'harems' of bachelors usually lasted for only a few days. All harem group bachelors, as well as some adult males, tolerated younger sexually mature bachelors at the group periphery. These younger bachelors defended the group, defecation marked, and urine marked, just as the dominant stallion did. However, they had no access to the females and did not try to herd them. Similar group constellations were observed in the Pryor Mountain population (Feist and McCullough 1976). On Bird Shoal-Carrot Island, I observed on several occasions subdominant stallions (bachelors) abandoning estrous-yearling females in favor of the group. Two same-aged bachelors switched leadership of a harem group several times over the course of six months.

This last phase of the investigated socialization period in males could be characterized as an intermediate state of development between sexual maturity (physiologically reproductive) and behavioral maturity (actually reproductive) in this population. This period lasted on the average about as long as the physiological maturation period (2 to 3 years).

Due to the abnormal sex distribution in other semi-feral horse populations, young males in the Camargue and New Forest were observed to mate at or right after sexual maturity, depending on the time of year (Tyler 1972, Wells and Goldschmidt-Rothschild 1979). In the truly feral Pryor Mountain horses, only the oldest bachelors formed harem groups (Feist and McCullough 1976). Lenarz (1980) found that bachelors of the feral horse population on Cumberland Island (Georgia, USA) began to form their own groups at the age of 5 to 7 years. Klingel (1965, 1969, 1972) and Estes (1974) describe that Grant's zebra and Grevy's zebra males reach sexual maturity at 2½ to 4 years, but are not reproductive until a year or two later. The plains zebra reached 'psychological maturity' at the age of 5 to 6 years, with the youngest family stallion being 5 to 6 years old.

Hardly any data are available on the reproductive activity in feral ass bachelors. Only Moehlman (1974) noted that a yearling copulated with an estrous female while no adult male was present. Personal observations in Central Australia (Hoffmann 1983) indicated that adult, dominant males temporarily accompanying estrous females prevented young males from mating.

Delayed onset of male reproduction is widespread in polygynous species (for example, elephant seals (LeBoeuf 1974), antelopes (Jarman and Jarman 1974, Gosling 1974) and in species with female family units with peripheral males (for example, chimpanzees (Van Lawick-Goddell 1971), Microcebus (Martin 1972), and Galago demidovii (Dominique 1972). In the Bird Shoal-Carrot Island horses, the time span between physical and actual reproductive status apparently served to provide the role-specific skills necessary to build up, lead, and defend a harem group and its members.

In concluding, it appears that male horses on Bird Shoal-Carrot Island go through several age-related phases of development in their socialization period. These phases differed in the occurrence, frequency, and distribution of behavior categories and patterns. According to Wiley (1980), these phases could also be regarded as functional positions in the given society. The transitions from an early position into a later position were irreversible. (Group stallions which had lost their group did not behave like mature bachelors, nor did they stay with them.) Males in different social environments within one position (for example, free-ranging bachelors versus same-aged harem group bachelors) showed differing sets of social behavior. It stills remains unanswered whether and how these different patterns of development, as well as intraposition hierarchies, may influence the individuals' reproductive success. It should be mentioned, though, that at one time or another between 1977 and 1982, every adult male was at least once in a stallion or subdominant stallion position during a breeding season.

I propose that functionally the bachelor groups on Bird Shoal-Carrot Island resemble the lek systems found in other herbivorous mammals (Estes 1969, Buechner and Roth 1974). A lek system may provide males a possibility of progression in rank and position towards a reproductive state. On Bird Shoal-Carrot Island, all immature males proceded through the various bachelor positions until they had reached reproductive age (5 to 7 years). The individual transitions from one position to another were partly elicited by external factors (for example, foal status to bachelor status was elicited by sibling presence or mature bachelor status to stallion status by the presence of females) and partly by internal factors (for example, yearling status to bachelor status was elicited by dispersal or immature bachelor status to mature bachelor status by sexual maturity). Among males, the successful acquisition of adult status occurred whether or not the animals displayed territoriality. The horses on Bird Shoal-Carrot Island showed no territoriality. On the other hand, bachelor groups, as well as territorial males, are found in other Equid species, such as wild asses and Grevy's zebra.

Therefore, it would be of great interest to compare this system of social development of males in a non-territorial population as presented in this study with the development of males in other Equid species that are territorial but that do not have a harem type of social organization. Although the social behavior patterns (the tools) are remarkably similar in all Equid males, the social ontogeny of the territorial species may take a completely different course of development than that found in the studied horse population. There are too few field studies to truly evaluate the correlations between a given social system and the social maturation of individuals. Hopefully, we will still be able to conduct such projects on feral and wild populations in the foreseeable future.

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